

Predicting how climate change will affect terrestrial mammals' movement and habitat selection 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} Siobhan Darlington^{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: 131

Words in main text: 4399

Figures: 7

Tables: 3

References: 73 (updated on 2025-01-16)

Appendices: 3

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

Abstract

Recent widespread warming has caused many terrestrial mammals to change when, how, and where they move, with cascading effects on individuals' fitness and habitat selection at the population, community, and ecosystem levels. Previous research has quantified the effects of temperature on mammalian movement behavior, but few have quantified the effects of future climate change on fine-scale movement and habitat selection. We address this gap by using Continuous-Time Movement Models and Hierarchical Generalized Additive Models to quantify the effects of temperature on mammal's probability of movement, speed, and habitat selection. We then leverage the estimated effects to predict when, how, and where mammals will move in BC throughout the 21st century. We conclude with implications for energetics, encounter rates, habitat conservation, and human-wildlife conflicts. **MISSING**

RESULTS AND CONCLUSIONS

Contents

Abstract	3
1 Introduction	5
2 Methods	9
2.1 Datasets	9
2.1.1 GPS telemetry data	9
2.1.2 Historical and projected temperature data	10
2.1.3 Resource rasters	11
2.2 Estimating mammals' instantaneous speeds	12
2.3 Estimating the effects of temperature on mammals' movement	12
2.3.1 Disentangling direct and indirect effects	12
2.3.2 Movement frequency and speed	13
2.3.3 Habitat selection	15
3 Results	16
3.1 Effects of temperature on movement rates	18
3.1.1 Predicted changes in movement during the current century	19
3.2 Effects of temperature on habitat selection	21
3.2.1 Predicted changes in movement during the current century	22
4 Discussion	23
4.1 Effects of temperature on mammals' movement	25
4.2 Effects of temperature on mammals' habitat selection	25
4.3 Considerations for future studies	25
4.4 Consequences for conservation	26
References	27

¹ 1 Introduction

² For most animals, movement is a rapid, low-cost, and low-risk response to a variety of
³ stimuli (Nathan *et al.*, 2008), including escaping predation (Peterson, Soto & McHenry,
⁴ 2021; Tan *et al.*, 2024; Bartashevich *et al.*, 2024), searching for resources (Charnov, 1976;
⁵ Mezzini *et al.*, 2024), and habitat selection (Kacelnik, Krebs & Bernstein, 1992; Winter *et*
⁶ *al.*, 2024). However, movement efficiency depends on ambient temperature, since it impacts
⁷ the energetic cost of movement (Taylor, Heglund & Maloij, 1982; Brown *et al.*, 2004; Jahn
⁸ & Seebacher, 2022), the ease of movement (e.g., snow depth and density, see Montgomery
⁹ *et al.*, 2019; Leclerc *et al.*, 2021; Melin *et al.*, 2023), and the risk of overheating (Heten
¹⁰ *et al.*, 2014; Dyer *et al.*, 2023). Additionally, temperature also affects movement indirectly
¹¹ by affecting other drivers of movement behavior, including physiology (Abram *et al.*, 2017),
¹² fitness (Berger *et al.*, 2018; Schmidt *et al.*, 2020), trophic interactions (Hegel *et al.*, 2010),
¹³ and the availability and value of resources (e.g., water and heat, see: Elmore *et al.*, 2017;
¹⁴ Attias *et al.*, 2018).

¹⁵ Changes in temperature affect not only whether and how fast animals move but also how
¹⁶ they move [i.e., speed and tortuosity; their movement behavior: Nathan *et al.* (2008); Dyer *et*
¹⁷ *al.* (2023)] and where they move to (habitat selection: Merkle *et al.*, 2016; Alston *et al.*, 2020;
¹⁸ Giroux *et al.*, 2023). Thus, temperature affects not only an animal's energetic expenditure
¹⁹ but also many other consequences of movement, including encounter rates with resources
²⁰ (Mezzini *et al.*, 2024), other animals (Martinez-Garcia *et al.*, 2020), and the occurrence of
²¹ human-wildlife conflict (Weststrate *et al.*, 2024). These changes are exacerbated at extreme
²² temperatures, as animals often alter their movement behaviors substantially when tempera-
²³ tures are excessively cold or hot (Wilson *et al.*, 2001; Berger *et al.*, 2018; Arechavala-Lopez *et*
²⁴ *al.*, 2019; Giroux *et al.*, 2023). But what counts as “extreme” varies across species: thermal
²⁵ specialists are more sensitive to small changes above or below their ideal range (Giroux *et*
²⁶ *al.*, 2023), while temperature generalists can adapt more easily to change (Dupont *et al.*,

27 2024). However, this greater adaptability is tested when generalists are subject to changes
28 that are more severe (McCain, 2019), affecting many factors (e.g., temperature, phenology,
29 and resource availability: Polazzo *et al.*, 2024), or too rapid to adapt to within the span of
30 a lifetime or a few generations (Levins, 1974; Fuller *et al.*, 2016; Xu *et al.*, 2021). Thus, it
31 remains unclear how or whether species will be able to respond to climate change in the cur-
32 rent century (Deb, Forbes & MacLean, 2020; Woo-Durand *et al.*, 2020; Verzuh *et al.*, 2023),
33 especially when populations do not react to changes in environmental conditions (Sawyer
34 *et al.*, 2019) or are physiologically incapable (Sherwood & Huber, 2010; Williams & Blois,
35 2018).

36 This uncertainty in both future conditions and their consequences on ecosystems and
37 populations presents a need for a comprehensive understanding of the effects of tempera-
38 ture on the movement of animal populations as well as the consequences this will have on
39 landscapes, biodiversity, and their adaptability and resiliency. Recent work has documented
40 climate-change-related changes mammals' ranges (Leclerc *et al.*, 2021), movement behavior
41 (Melin *et al.*, 2023); thermoregulation (Mota-Rojas *et al.*, 2021), and trait-based responses
42 (McCain, 2019), but it is still unclear how mammals will adapt their small-scale movement
43 and habitat selection to future changes in temperature (Intergovernmental Panel On Climate
44 Change, 2023; but see Hetem *et al.*, 2014; Winter *et al.*, 2024). In the last 200 years, many
45 ecosystems experienced widespread warming that resulted in milder and shorter winters,
46 hotter and longer summers, and a greater risk of extremely high temperatures and severe
47 forest fires (Zurowski, 2023; Intergovernmental Panel On Climate Change, 2023). Over the
48 next 100 years, these changes will worsen and continue to impact mammals' fitness, move-
49 ment behavior, and habitat selection as they cope with growing heat stress (Deb *et al.*, 2020;
50 Woo-Durand *et al.*, 2020) and frequency and intensity of extreme events (Bunnell, Kremsater
51 & Wells, 2011) along with growing anthropogenic pressure (Sawyer *et al.*, 2009; Sih, Ferrari
52 & Harris, 2011; Weststrate *et al.*, 2024).

53 Understanding the direct and indirect impacts of temperature on mammalian movement

54 is essential for decision makers to be able to prepare and respond to change in a proac-
55 tive manner (e.g., Sawyer *et al.*, 2009; McCain, 2019). The Canadian province of British
56 Columbia is currently experiencing rapid widespread warming, phenological shifts, and more
57 frequent and intense extreme events, including forest fires (Zurowski, 2023). In light of the
58 “30 by 30” conservation initiative, a global effort to conserve 30% of the world’s lands and
59 oceans by 2030 (Section H, Targets 2 and 3 of Convention on Biological Diversity, 2022),
60 we stress that decision makers must understand which areas will be of greatest value for
61 maximizing the project’s effectiveness. Predicting how climate change will affect how, when,
62 and where animals will move is necessary for identifying which landscapes are most valuable
63 now as well as in the future. Failing to understand how changes in temperature will affect
64 mammalian movement behavior and habitat selection will hinder our ability to respond to
65 the current climate crisis and make decisions that are viable in the long term.

66 This paper provides an analysis of the effects of spatiotemporally proximal temperature
67 on the movement of six terrestrial mammal species in British Columbia (BC), Canada (*Ca-*
68 *nis lupus*, *Cervus canadensis*, *Oreamnos americanus*, *Puma concolor*, boreal and southern
69 mountain *Rangifer tarandus*, and *Ursus arctos horribilis*; Table 1). Using over two decades
70 of telemetry data over a large spatial range of British Columbia (Fig. 1) and hourly air
71 temperature data, we estimate how mammals altered their movement frequency, movement
72 speed, and habitat selection in response to temperature. We then pair the estimated re-
73 sponses with climate change projections to forecast changes in mammalian movement in the
74 current century under different climate-change scenarios (Shared Socioeconomic Pathways,
75 see Riahi *et al.*, 2017). We discuss the consequences of these changes in movement behavior
76 with regards to energetics, encounter rates, habitat conservation, and human-wildlife con-
77 flicts while disentangling the direct and indirect effects of temperature on the movement
78 behavior of terrestrial mammals.

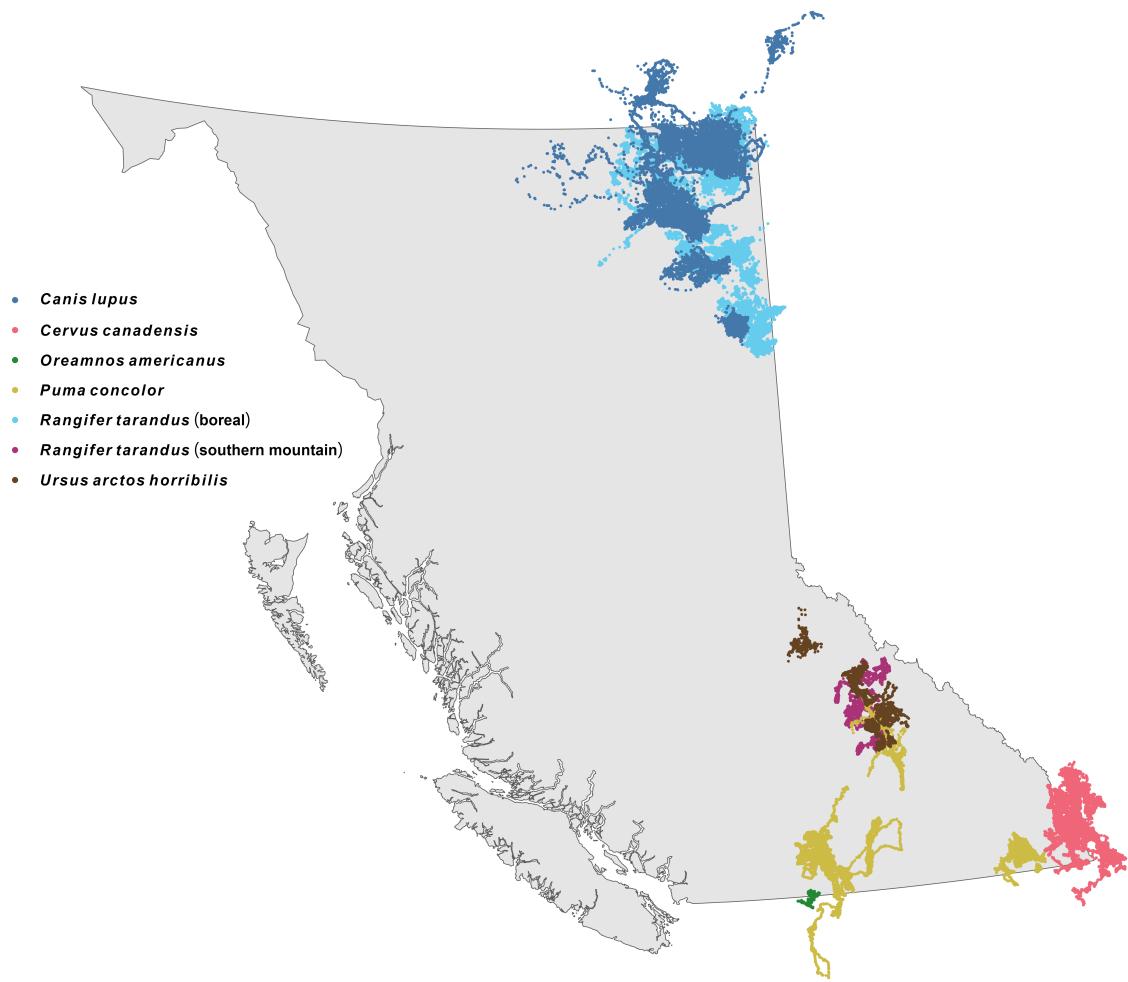


Figure 1: GPS telemetry data for the six species in this study.

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

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

79 2 Methods

80 2.1 Datasets

81 This manuscript leverages four main datasets: (1) a collection of GPS telemetry data;
 82 (2) historical hourly reanalyzed air temperature from the ERA5 dataset from the European
 83 Center for Medium-range Weather Forecasting; (3) resource rasters of percent forest cover,
 84 elevation, and distance from water; and (4) climate change projections under four Shared
 85 Socioeconomic Pathways (SSPs, see Riahi *et al.*, 2017). We detail the data sources and
 86 analyses in the sections below, and more details are available in appendices A (estimating how
 87 temperature affects movement frequency and speed when moving), B (fitting Hierarchical
 88 Resource Selection Functions), and C (simulating hourly temperature data to 2100 using the
 89 four SSPs).

90 2.1.1 GPS telemetry data

91 Elk (*Cervus canadensis*) data from Ciuti *et al.* (2012) were downloaded from Movebank
 92 (study name: Elk in southwestern Alberta, see Kays *et al.*, 2022), while boreal caribou

93 (Rangifer tarandus) and wolf (Canis lupus) telemetries were acquired via a public BC Oil and
94 Gas Research and Innovation Society repository (<https://www.bcogrism.ca/projects/boreal->
95 caribou-telemetry-data). Clearly erroneous GPS locations were removed using diagnostic
96 plots of (1) distance from the median location, (2) straight-line displacement between loca-
97 tions, (3) turning angle, and (4) time interval between consecutive points. Particular atten-
98 tion was paid to points with large turning angles ($\gtrapprox 170^\circ$) and excessively high straight-line
99 displacement, especially if antecedent and subsequent points indicated stationary behavior.
100 The script used to clean the data and all associated custom functions are available on GitHub
101 at <https://github.com/QuantitativeEcologyLab/bc-mammals-temperature>.

102 2.1.2 Historical and projected temperature data

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

109 We obtained rasters of projected monthly average temperature at a 0.08° resolution in BC
110 from 2020 to 2100 under the different SSPs via the `climatenetR` package (version 1.0, Burnett,
111 2023) for R. Since the climate projections only provided monthly means and ranges but no
112 measures of variance or distributional assumptions, we used the hourly ERA5 data for BC
113 from 1998 to 2023 (extremes included, see Hersbach *et al.*, 2023) to calculate within-month
114 variance in temperature, which we defined as the variance within a given pixel, month, and
115 year. We then modeled the estimated variance using a GAM for location and scale (GAMLS,
116 see: Rigby & Stasinopoulos, 2005; Stasinopoulos & Rigby, 2007; section 7.9 in Wood, 2017).
117 The linear predictor for the location (i.e., the mean) included smooth terms of the within-
118 pixel monthly mean temperature (within each year), month (as a cyclic smooth), a two-

119 dimensional smooth of space, and a tensor interaction product term of space and month. The
120 linear predictor for the scale term (which governs the mean-variance relationship) included
121 smooth terms of the monthly mean, month, and space. We did not include a smooth of
122 year to avoid unrealistic projections when extrapolating beyond the range of historical data.
123 Additional details are available in Appendix C.

124 We simulated hourly variation in weather by assuming temperature followed a normal
125 distribution with mean specified by the monthly `climatenar` climate projections and vari-
126 ance as specified by the Gamma GMLS. We then predicted changes in movement behavior
127 and habitat selection as a function of the simulated temperature using the HGAMs and
128 HRSFs. For each month within each year from 2020 to 2100, we simulated hourly weather
129 by including temperatures from the 0.1 to the 0.9 quantile by increments of 0.1, and we
130 weighted each quantile proportionally to the (normalized) Gaussian probability density for
131 each quantile (Appendix C).

132 2.1.3 Resource rasters

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

145 **2.2 Estimating mammals' instantaneous speeds**

146 We modeled each animal's movement using continuous-time movement models (Fleming *et*
147 *al.*, 2014) via the `ctmm` package (version 1.2.0, Fleming & Calabrese, 2023) for R. We then
148 estimated mammals' instantaneous speeds by applying the `ctmm::speeds()` function on all
149 models with finite speed estimates (415 of 433, see Fleming *et al.*, 2014; Noonan *et al.*,
150 2019a). The 18 telemtries with insufficiently fine sampling were for one mountain goat, 15
151 boreal caribou, and 2 southern mountain caribou (Table 1).

152 Since `ctmm`'s movement models assume stochastic but non-zero speeds (i.e., a single,
153 stochastic moving state), data-informed speeds needed to be corrected so that the minimum
154 instantaneous speed could be 0. We performed this correction by subtracting each model's
155 mean speed while assuming speeds were χ^2 -distributed. The function we used is avail-
156 able on GitHub at <https://github.com/QuantitativeEcologyLab/bc-mammals-temperature/>
157 blob/main/functions/detrend_speeds.R. To avoid artifacts due to excessively small, non-
158 zero speeds, we determined whether an animal was moving or not using the inflection point
159 of each species' histogram of detrended speed estimates (Appendix A).

160 **2.3 Estimating the effects of temperature on mammals' movement**

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

166 **2.3.1 Disentangling direct and indirect effects**

167 In this manuscript, we separate the effects of temperature on mammalian movement into
168 indirect and direct effects. We call "indirect" all effects that can be intervened on by altering
169 an animal's habitat (its geographic space *sensu* Matthiopoulos, 2022), 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 behavior 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* Matthiopoulos, 2022), so it is not possible to mitigate the effects of temperature on movement behavior (other than changing temperature directly). We provide Directed Acyclical Graphs in Appendix A (modeling the effects of temperature on movement rates), and Appendix B (modeling the effects of temperature on habitat selection).

2.3.2 Movement frequency and speed

We estimated the effects of temperature on mammals’ movement state (moving or not) and speed (when moving) using two Hierarchical Generalized Additive Models (HGAMs, see Pedersen *et al.*, 2019 and the code chunk below) with the `mgcv` package for R (version 1.9-1, Wood, 2017). The first HGAM estimated the probability that an animal was moving with a binomial family of distributions and logit link function. The second HGAM estimated an animal’s speed (when moving) with a gamma family of distributions and log link function. The HGAMs included random intercepts for each animal (`s(..., bs = 're')`), fixed-effect intercepts for each species, and species-level `by` smooths for time of day, day of year, and temperature (`s(..., by = species)`), see model I in Figure 4 of Pedersen *et al.*, 2019). Additionally, the models had three tensor product interaction terms (`ti()`) for each species: (1) day of year and time of day, (2) temperature and time of day, and (3) temperature and day of year. These three terms accounted for: (1) seasonal changes in day length, (2) hourly changes in the response to temperature (e.g., changes in nocturnality), and (3) seasonal changes in the response to temperature (e.g., changes in coats and migration timing). The HGAMs accounted for the cyclicity of time of day and day of year using cyclic cubic splines

196 (`bs = 'cc'`, Wood, 2017). Together, the binomial HGAM and the gamma HGAM inform
 197 us on an animal's long-term average speed, since it is the product of the probability of
 198 moving and its average speed when moving. We fit the models with fast REML ('fREML')
 199 and discretized covariates (`discrete = TRUE`) to optimize computational efficiency with no
 200 appreciable losses to model performance (Wood, Goude & Shaw, 2015; Wood *et al.*, 2017;
 201 Li & Wood, 2020). Additional details are provided in Appendix A.

```

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

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

```

202 2.3.3 Habitat selection

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

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

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

3 Results

Species differed in mean probabilities of movement (range: 0.05 – 0.27), mean speed when moving (range: 0.42 – 2.67 km/day), and mean distance travelled (range: 0.04 – 0.62 km/day) even after post-stratifying to a sampling interval of one hour (Tab. 2). The inclusion of temperature in the model did not affect any of the three measures substantially when post-stratifying to 0°C. Grizzly bears tended to move least often ($P(M = 1) \approx 0.05$), while wolves and pumas moved most often ($P(M = 1) \geq 0.23$), and wolves had the highest mean speed when moving. Consequently, wolves traveled 3.0 to 15.6 times further per day than other mammals, on average.

- CHANGED FOREST RASTER TO USE ALL TREE TYPES (2025-01-17)
- NEED TO REMAKE HRSF FIGURES

THIS IS FALSEWe did not find any consistent selections for or against forest cover, but all species exhibited stronger selection preferences for elevation and distance from water than for forest cover, and there was no consistent preference for forest cover across tem-

239 peratures. In contrast, all species showed a strong preference for specific altitudes: wolves,
 240 pumas, and boreal caribou generally preferred elevations < 1 km above sea level, while elk,
 241 mountain goats, southern mountain caribou, and grizzly bears generally preferred elevations
 242 between 1 and 2 km above sea level. All species except for elk and grizzly bears preferred
 243 being as close to water as possible,

244 Overall, we did not detect any strong selections for or against forest cover, and this lack of
 245 preference was generally true irrespective of temperature. In contrast, we selection strength
 246 for forest cover did not vary strongly with temperature,

247 preferred resources

248 **CHECK TABLE 2: UPDATE AFTER REMOVING SCEK014 AND**
 249 **SCEK014b (2024-11-19 9:50)**

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

Species	$P(M)$	$P(M T)$	$\mathbb{E}(S M = 1)$	$\mathbb{E}(S M = 1, T)$	$\mathbb{E}(D)$	$\mathbb{E}(D T)$
<i>Canis lupus</i>	0.23	0.22	2.64	2.67	0.61	0.60
<i>Cervus canadensis</i>	0.16	0.17	0.57	0.57	0.09	0.10
<i>Oreamnos americanus</i>	0.15	0.13	0.43	0.42	0.06	0.06
<i>Puma concolor</i>	0.27	0.31	0.74	0.76	0.20	0.24
<i>R. tarandus</i> (boreal)	0.19	0.18	0.71	0.73	0.14	0.13
<i>R. tarandus</i> (s. mountain)	0.11	0.11	0.43	0.42	0.05	0.05
<i>Ursus arctos horribilis</i>	0.05	0.05	0.72	0.72	0.04	0.04

250 For most models, including smooth terms of temperature did not always improve within-
 251 sample prediction substantially (change in deviance explained: $+0.2\% - +17.9\%$), and there

252 was relatively strong agreement between models with and without temperature (Fig. ***SX***
253 ***pred vs pred***), but including temperature resulted in substantially better fits for all models
254 (all $\Delta\text{AIC} \leq -326$; Table 3).

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

Model	Species	ΔDE	ΔAIC
P(moving)	All	0.5%	-5927
Speed	All	0.2%	-1682
HRSF	Canis lupus	10%	-7200
HRSF	Cervus canadensis	4.5%	-4305
HRSF	Oreamnos americanus	17.6%	-769
HRSF	Puma concolor	7.8%	-945
HRSF	Rangifer tarandus (boreal)	5.9%	-6284
HRSF	Rangifer tarandus (s. mountain)	11.8%	-326
HRSF	Ursus arctos horribilis	17.9%	-920

255 **3.1 Effects of temperature on movement rates**

256 The partial effects of temperature varied in both direction and magnitude across species
257 (Fig. ***AX***), even after accounting for differences in daily and seasonal activity (e.g., sleep-
258 ing, migration, hibernation; see Fig. ***AX***). Smooth interaction terms were well-behaved
259 and indicated clear shifts in daily activity for all species (Fig. ***AX***). The models explained
260 reasonably high proportions of the deviance (11% for the binomial model and 79% for the
261 Gamma model) and had good in-sample prediction (Fig. ***AX***). Both movement frequency
262 and speed when moving decreased with increasing sampling interval, with a strong common
263 effect (Fig. ***AX***). Most species adapted their daily and seasonal movement behavior to

changes in temperature (Fig. 2), but the precision of the estimated change depends on the GPS sampling frequency. While `ctmm` models are scale independent (Noonan *et al.*, 2019a), the accuracy, size, and stability of speed estimates still depends on the GPS sampling frequency. This is because coarser sampling contains information on large scale movements (e.g., range crossings, migrations) but not fine-scale movement (e.g., first-order habitat selection). Using the boreal caribou as an example, the 13-hour sampling interval allows us to reasonably estimate the caribou's movement path at a temporal scale of approximately 13 hours (or greater), but we cannot produce reasonable movement trajectories at a much finer (e.g., hourly) scale. Consequently, the estimated movement behaviors should be compared across species carefully.

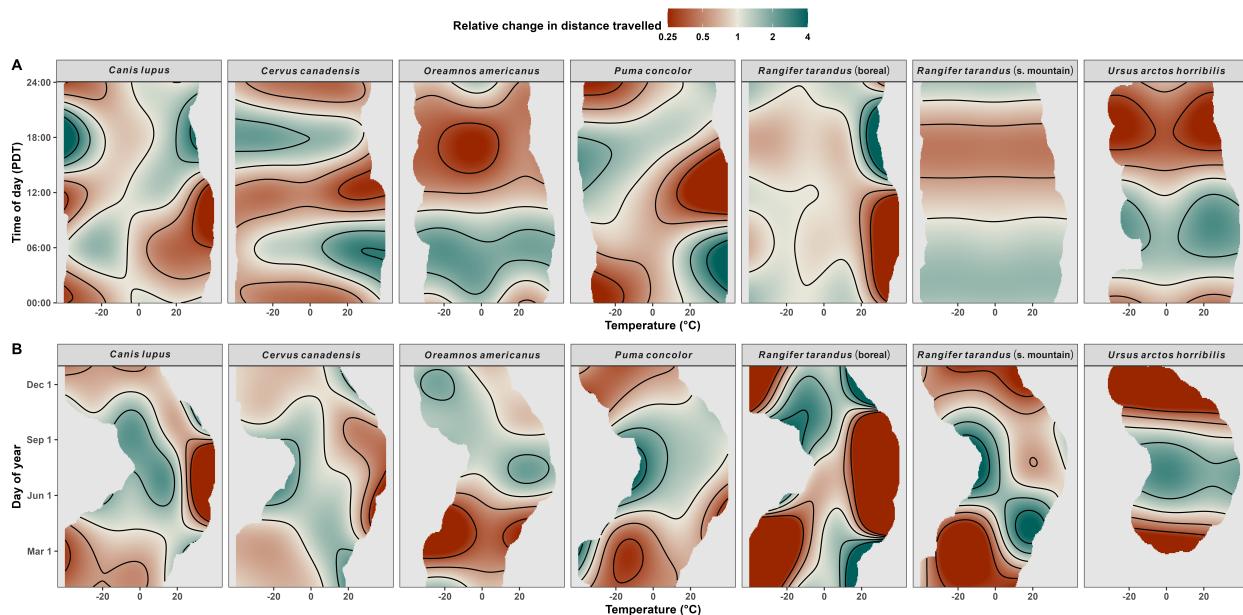


Figure 2: Temperature is a strong determinant of how far and when mammals travel. The fill indicates the estimated effects of temperature on the relative change in distance travelled (probability of moving times mean speed when moving) over time of day (**A**) and day of year (**B**). Predictions in the surface plots extend to 10% of the range away from each datum. The color bar is on the \log_2 scale to help visualize patterns in doubling, and values are capped to -75% and +300% for ease of readability.

274 3.1.1 Predicted changes in movement during the current century

275 The direction and degree of change in distance travelled varies greatly between species,
 276 but worse climate-change scenarios consistently corresponded to greater absolute changes in
 277 behavior as well as greater uncertainty in the estimated change (Fig. 3). Under the best-

case scenario, absolute projected changes by 2100 were small (0% to 2%, except for southern mountain caribou, which had a change of ~5%). Under the worst-case scenario, absolute projected changes were by 2100 ranged from ~1% (boreal caribou) to ~25% (southern moutain caribou) and had the greatest uncertainty in the estimates. Boreal caribou and elk showed relatively little projected changes, especially relative to the degree of inter-annual variability in distance travelled.

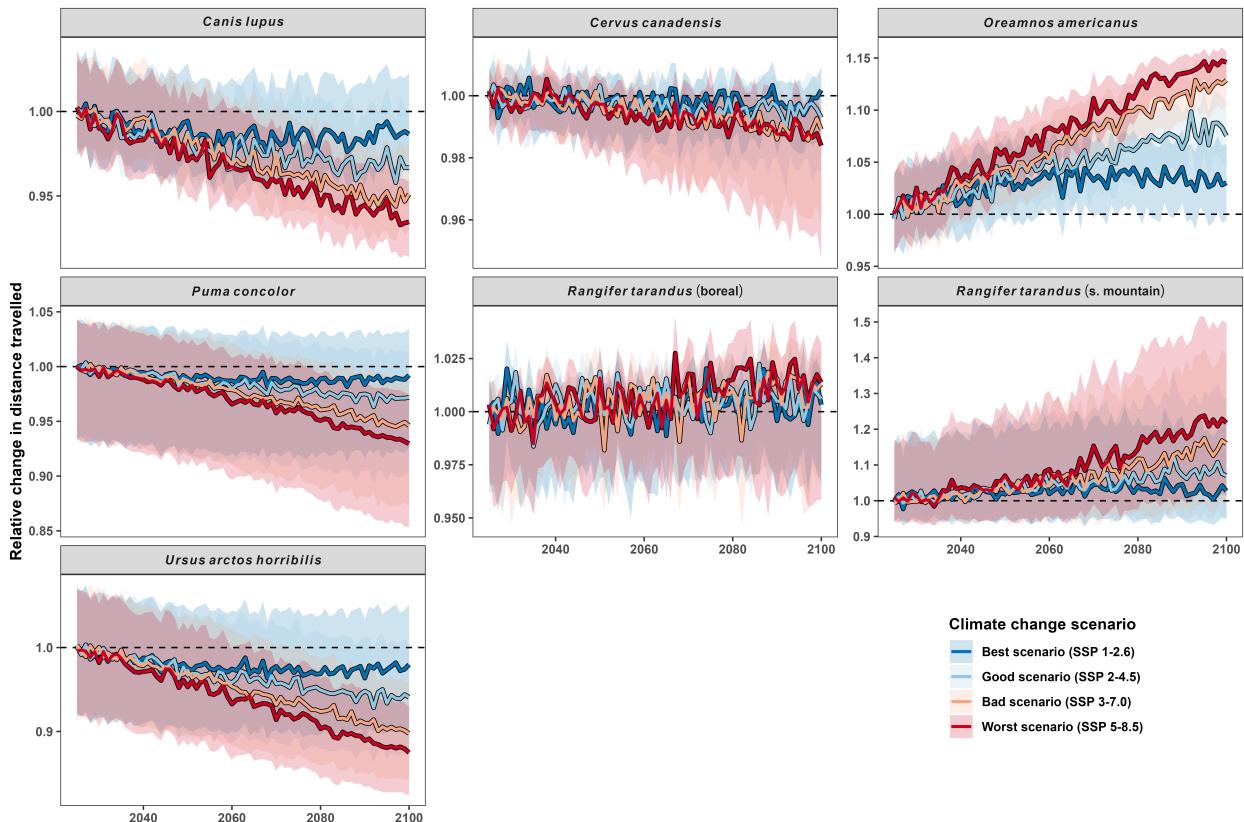
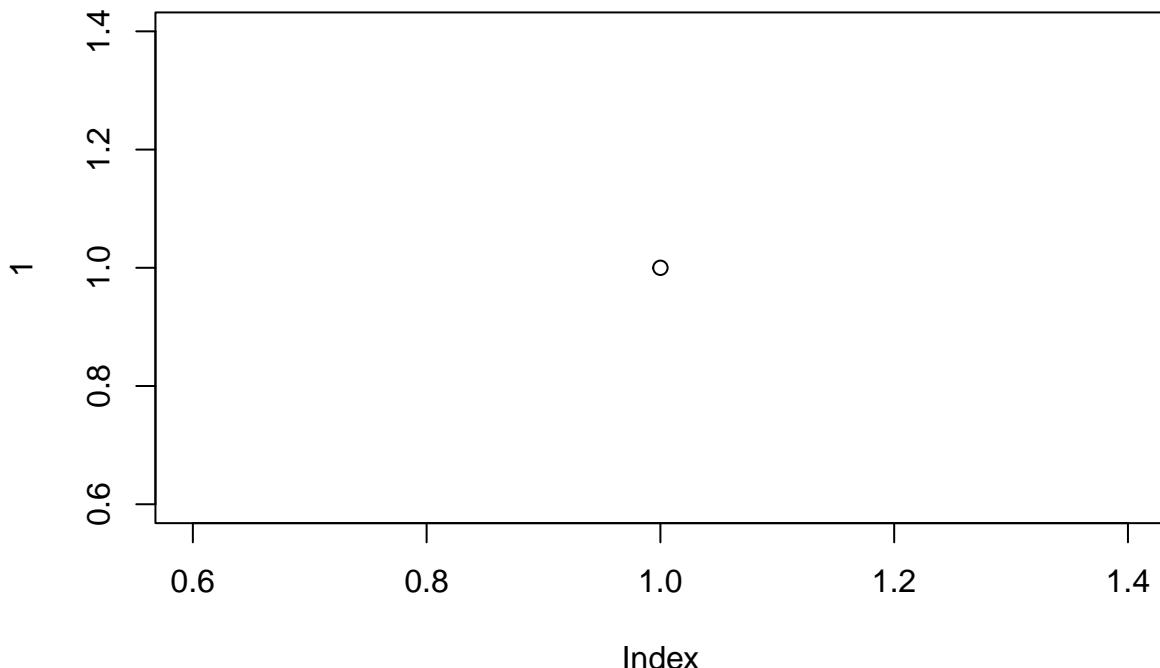


Figure 3: The intensity and direction of changes in movement rates due to climate change varies among species, but worse climate-change scenarios often result in the greatest change and greatest uncertainty. Lines indicate the projected relative change in mean distance travelled (probability of moving times speed when moving) due to changes in temperature within the species' current extent. Shaded areas indicate the mean 95% Bayesian credible intervals. Changes are relative to the mean distances travelled in 2020 across the four Shared Socioeconomic Pathways (SSPs). The SSPs are listed in order of similarity to current conditions, from SSP 1-2.6 (sustainability, best-case scenario) to 5-8.5 (fossil-fueled development, worst-case scenario). The projections only account for changes movement behavior (i.e., movement frequency and speed) and ignore changes in physiology or movement costs.

284 COMMENTS ABOUT SPATIAL VARIATION IN *distance travelled*

4. spatial projections of distance in 2020 and 2100



285

286 3.2 Effects of temperature on habitat selection

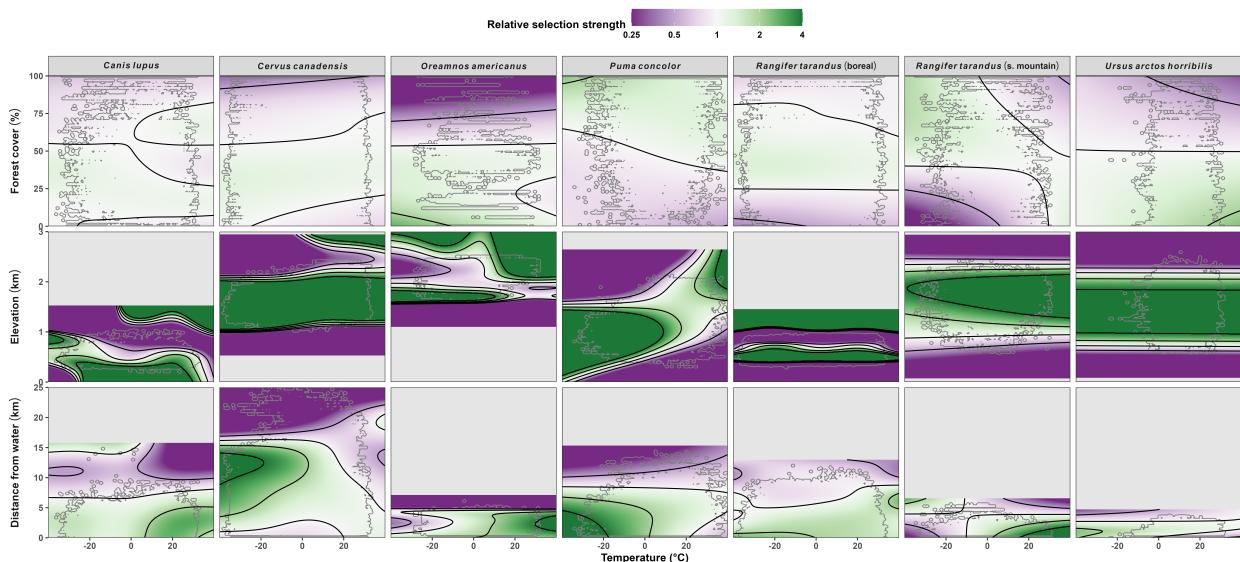


Figure 4: Temperature strongly affects mammals' habitat selection. Estimated resource selection strength for forest cover (%), elevation (km), and distance from water (km) as a function of temperature. The grey contours indicate the extent of each species' observed locations.

²⁸⁷ 3.2.1 Predicted changes in movement during the current century

6. temporal projections of RSFs within current area

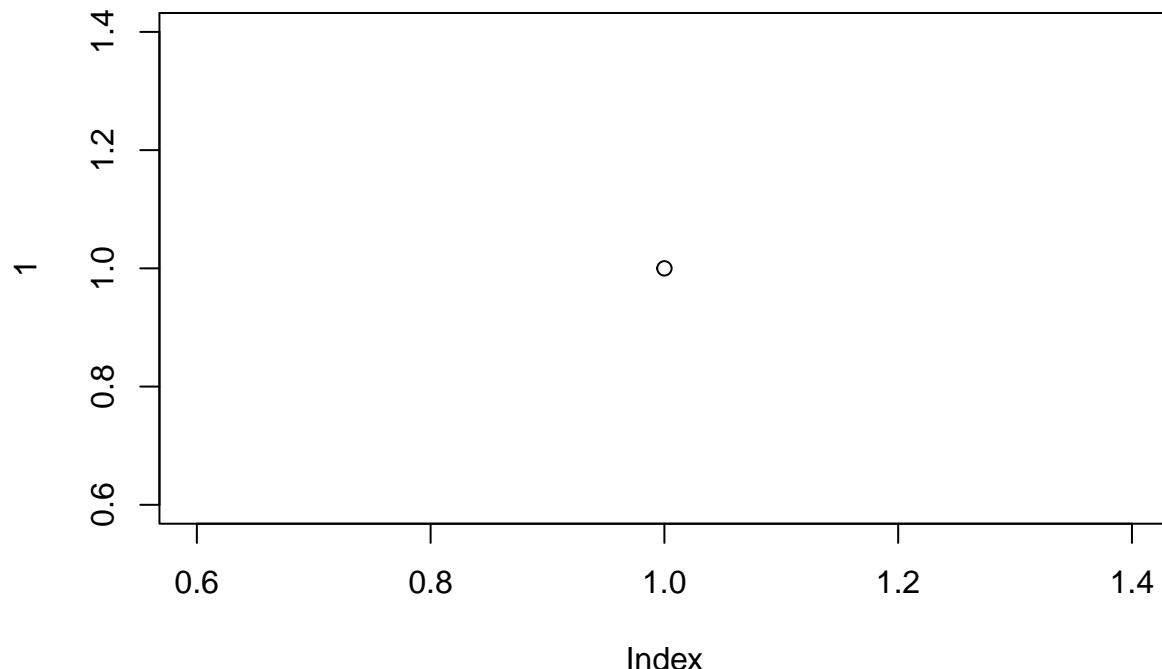
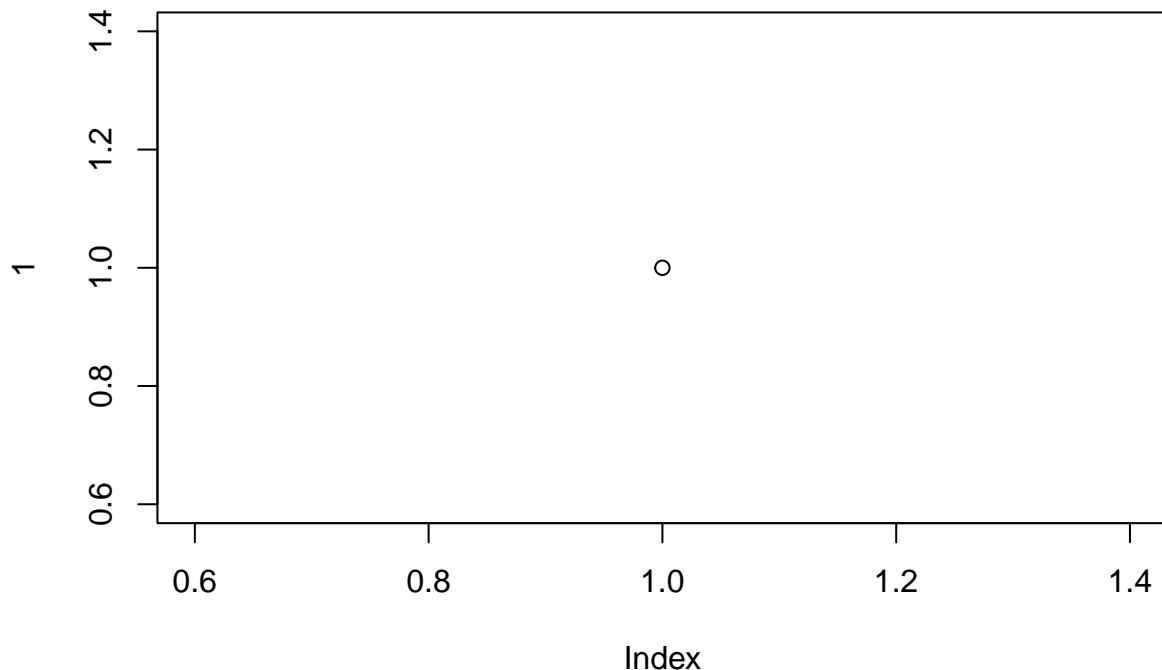


Figure 5: The intensity and direction of changes in habitat selection due to climate change vary among species, but worse climate-change scenarios consistently result in the greatest change and greatest uncertainty. Lines indicate the projected change in relative selection strength for forest cover (%), elevation (km), and distance from water (km) due to changes in temperature within the species' current extent. Shaded areas indicate the mean 95% Bayesian credible intervals. Changes are relative to the relative selection strength in 2020 across the four Shared Socioeconomic Pathways (SSPs). The SSPs are listed in order of similarity to current conditions, from SSP 1-2.6 (sustainability, best-case scenario) to 5-8.5 (fossil-fueled development, worst-case scenario).

7. spatial projections of RSFs in 2020 and 2100



288

289 4 Discussion

290 We demonstrated that temperature is an important determinant of how and where mam-
291 mals move, even while accounting for other seasonal drivers of movement (e.g., changes in
292 photoperiod, hormones, and resources). This is important because decoupling temperature
293 from other drivers allows us to predict how changes in climate will affect mammalian move-
294 ment even if all other drivers remain constant.

- 295 • We discuss the consequences of these changes in movement behavior with regards to
296 energetics, encounter rates, habitat conservation, and human-wildlife conflicts.
- 297 • as temperatures get warmer, we will be pushing into the unknown portion of the surface
298 plots

- 299 • our models don't include any physiological responses to temperature that may impact
300 movement (e.g., hibernation)
- 301 • our models also assume the behaviour we modeled now will persist into the future
302 (e.g., hibernation, migration)
- 303 • based on the model, temperature doesn't affect grizzlies' hibernation much, and their
304 distance travelled in winter is very low due to $P(\text{moving})$ being so low:
- 305 • if the RSS decreases a lot, individuals may disperse, populations may relocate, or stay
306 where they are and suffer
- 307 • RSFs require good data coverage over the resource-temperature space
- 308 • future work investigating effects on a single species or evaluating space more accurately
309 should:
- 310 • use fully Bayesian models with appropriate regularizing priors and penalties to avoid
311 excessive predictions
- 312 • use B splines to specify better penalty spaces
- 313 • have more data with good coverage over the covariate space
- 314 • Pease (2024): the scale at which we measure variables affects their estimated effect
- 315 • Hetem *et al.* (2014):
- 316 • rate of climate change is too fast for genetic adaptation to occur in mammals with
317 longevities of decades
- 318 • example of suitable habitat prediction to 2050
- 319 • proactive conservation: Sawyer *et al.* (2009)

320 **4.1 Effects of temperature on mammals' movement**

321 **4.2 Effects of temperature on mammals' habitat selection**

322 **4.3 Considerations for future studies**

323 Our work highlights **X** central considerations for future research: (1) telemetry sampling
324 rates should be designed primarily in relation to the movement timescales of the species of
325 interest and ideally with multiple samples **path?**, (2) the number of individuals tracked and
326 the length of each telemetry should depend on environmental stability, and (3) **projecting**
327 **into the fringes***

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

338 When landscapes are relatively predictable across years, a larger number of sampled in-
339 dividuals is likely preferable over longer, multi-year telemtries. This allows one to quantify
340 the variance across individuals, including the range of conditions and environments that
341 individual animals are in. A good estimate of inter-individual variance provides better co-
342 efficient estimates along with more appropriate measures of uncertainty. However, when
343 conditions across years are relatively stochastic, multi-year telemtries allow one to better
344 estimate inter-annual and inter-individual variation. In either case, carefully-designed sam-
345 pling schedules and (Bayesian) hierarchical models can provide good estimates of the effects

346 of interested along with appropriate measures of uncertainty (McElreath, 2016).

- 347 • improve projections at the edges of the HRSFs with local and Traditional Knowledge
348 (Kutz & Tomaselli, 2019)
- 349 • changes in temperatures are pushing to areas in the surface plots that have little
350 data and may be poorly estimated. We will need to extrapolate to prepare for future
351 changes, which implies some degree of inevitable risk. The best way to avoid this is by
352 designing models that are statistically sound and interpretable. The models we present
353 provide an estimate of the changes in behavior, but they are not tailored specifically
354 to any of the species in the dataset. Species-specific models should account for more
355 particular variables (e.g., forest age for caribou) and use dynamic resource rasters (i.e.,
356 not use a static estimate of forest cover). Nonetheless, we present important results for
357 understanding how mammals will respond to changes in climate and weather during
358 the next ~75 years.

359 **4.4 Consequences for conservation**

- 360 • energetics
- 361 • encounter rates (lower encounter rates with food (Hou *et al.*, 2020))
- 362 • HWI (Weststrate *et al.*, 2024) z* Machine Learning (Generative Artificial Intelligence;
363 GenAI) AI is fueling climate change. We need to proactively prepare to respond to
364 climate change. Pollution is not under the control of the masses, so predicting change
365 will be hard
- 366 • high energy and water demands (Li *et al.*, 2023) GenAI consumption of water
- 367 • high carbon footprint (Luccioni, Viguer & Ligozat, 2024)
- 368 • Pollution is not under control of the masses, so predicting change will be hard

³⁶⁹ **References**

- ³⁷⁰ Aarts G., MacKenzie M., McConnell B., Fedak M. & Matthiopoulos J. (2008). Estimating
³⁷¹ space-use and habitat preference from wildlife telemetry data. *Ecography* **31**, 140–160.
³⁷² <https://doi.org/10.1111/j.2007.0906-7590.05236.x>
- ³⁷³ Abram P.K., Boivin G., Moiroux J. & Brodeur J. (2017). Behavioural effects of temper-
³⁷⁴ ature on ectothermic animals: Unifying thermal physiology and behavioural plasticity.
³⁷⁵ *Biological Reviews* **92**, 1859–1876. <https://doi.org/10.1111/brv.12312>
- ³⁷⁶ Alston J.M., Fleming C.H., Kays R., Streicher J.P., Downs C.T., Ramesh T., *et al.* (2022).
³⁷⁷ Mitigating pseudoreplication and bias in resource selection functions with autocorrela-
³⁷⁸ tion-informed weighting. *Methods in Ecology and Evolution*, 2041–210X.14025. <https://doi.org/10.1111/2041-210X.14025>
- ³⁸⁰ Alston J.M., Joyce M.J., Merkle J.A. & Moen R.A. (2020). Temperature shapes movement
³⁸¹ and habitat selection by a heat-sensitive ungulate. *Landscape Ecology* **35**, 1961–1973.
³⁸² <https://doi.org/10.1007/s10980-020-01072-y>
- ³⁸³ Arechavala-Lopez P., Minguito-Frutos M., Follana-Berná G. & Palmer M. (2019). Common
³⁸⁴ octopus settled in human-altered mediterranean coastal waters: From individual home
³⁸⁵ range to population dynamics. *ICES Journal of Marine Science* **76**, 585–597. <https://doi.org/10.1093/icesjms/fsy014>
- ³⁸⁷ Attias N., Oliveira-Santos L.G.R., Fagan W.F. & Mourão G. (2018). Effects of air temper-
³⁸⁸ ature on habitat selection and activity patterns of two tropical imperfect homeotherms.
³⁸⁹ *Animal Behaviour* **140**, 129–140. <https://doi.org/10.1016/j.anbehav.2018.04.011>
- ³⁹⁰ Bartashevich P., Herbert-Read J.E., Hansen M.J., Dhellemmes F., Domenici P., Krause J.,
³⁹¹ *et al.* (2024). Collective anti-predator escape manoeuvres through optimal attack and
³⁹² avoidance strategies. *Communications Biology* **7**, 1586. <https://doi.org/10.1038/s42003-024-07267-2>
- ³⁹⁴ Berger J., Hartway C., Gruzdev A. & Johnson M. (2018). Climate degradation and extreme

- 395 icing events constrain life in cold-adapted mammals. *Scientific Reports* **8**, 1156. <https://doi.org/10.1038/s41598-018-19416-9>
- 396
- 397 Brown J.H., Gillooly J.F., Allen A.P., Savage V.M. & West G.B. (2004). Toward a metabolic
- 398 theory of ecology. *Ecology* **85**, 1771–1789. <https://doi.org/10.1890/03-9000>
- 399 Bunnell F.L., Kremsater L.L. & Wells R.W. (2011). Global weirding in british columbia:
- 400 Climate change and the habitat of terrestrial vertebrates. *Journal of Ecosystems and*
- 401 *Management* **12**. <https://doi.org/10.22230/jem.2011v12n2a74>
- 402 Burnett M. (2023). *climatenaR: Tools to access ClimateNA data.*
- 403 Charnov E.L. (1976). Optimal foraging, the marginal value theorem. *Theoretical Population*
- 404 *Biology* **9**, 129–136. [https://doi.org/10.1016/0040-5809\(76\)90040-X](https://doi.org/10.1016/0040-5809(76)90040-X)
- 405 Ciuti S., Muhly T.B., Paton D.G., McDevitt A.D., Musiani M. & Boyce M.S. (2012). Human
- 406 selection of elk behavioural traits in a landscape of fear. *Proceedings of the Royal Society*
- 407 *B: Biological Sciences* **279**, 4407–4416. <https://doi.org/10.1098/rspb.2012.1483>
- 408 Convention on Biological Diversity (2022). 15/4. Kunming-montreal global biodiversity
- 409 framework
- 410 Deb J.C., Forbes G. & MacLean D.A. (2020). Modelling the spatial distribution of selected
- 411 north american woodland mammals under future climate scenarios. *Mammal Review* **50**,
- 412 440–452. <https://doi.org/10.1111/mam.12210>
- 413 Dupont L., Thierry M., Zinger L., Legrand D. & Jacob S. (2024). Beyond reaction norms:
- 414 The temporal dynamics of phenotypic plasticity. *Trends in Ecology & Evolution* **39**,
- 415 41–51. <https://doi.org/10.1016/j.tree.2023.08.014>
- 416 Dyer A., Brose U., Berti E., Rosenbaum B. & Hirt M.R. (2023). The travel speeds of large
- 417 animals are limited by their heat-dissipation capacities. *PLOS Biology* **21**, e3001820.
- 418 <https://doi.org/10.1371/journal.pbio.3001820>
- 419 Elmore R.D., Carroll J.M., Tanner E.P., Hovick T.J., Grisham B.A., Fuhlendorf S.D., *et*
- 420 *al.* (2017). Implications of the thermal environment for terrestrial wildlife management.
- 421 *Wildlife Society Bulletin* **41**, 183–193. <https://doi.org/10.1002/wsb.772>

- 422 Fleming C.H. & Calabrese J.M. (2017). A new kernel density estimator for accurate
423 home-range and species-range area estimation. *Methods in Ecology and Evolution* **8**,
424 571–579. <https://doi.org/10.1111/2041-210X.12673>
- 425 Fleming C.H. & Calabrese J.M. (2023). *Ctmm: Continuous-time movement modeling*.
- 426 Fleming C.H., Calabrese J.M., Mueller T., Olson K.A., Leimgruber P. & Fagan W.F. (2014).
427 From fine-scale foraging to home ranges: A semivariance approach to identifying move-
428 ment modes across spatiotemporal scales. *The American Naturalist* **183**, E154–E167.
429 <https://doi.org/10.1086/675504>
- 430 Fuller A., Mitchell D., Maloney S.K. & Hetem R.S. (2016). Towards a mechanistic under-
431 standing of the responses of large terrestrial mammals to heat and aridity associated with
432 climate change. *Climate Change Responses* **3**, 10. [https://doi.org/10.1186/s40665-016-0024-1](https://doi.org/10.1186/s40665-016-
433 0024-1)
- 434 Giroux A., Ortega Z., Attias N., Desbiez A.L.J., Valle D., Börger L., *et al.* (2023). Activ-
435 ity modulation and selection for forests help giant anteaters to cope with temperature
436 changes. *Animal Behaviour* **201**, 191–209. [https://doi.org/10.1016/j.anbehav.2023.04.008](https://doi.org/10.1016/j.anbehav.2023.04.
437 008)
- 438 Hegel T.M., Mysterud A., Huettmann F. & Stenseth N.C. (2010). Interacting effect of
439 wolves and climate on recruitment in a northern mountain caribou population. *Oikos*
440 **119**, 1453–1461. <https://doi.org/10.1111/j.1600-0706.2010.18358.x>
- 441 Hersbach H., Bell B., Berrisford P., Biavati G., Horányi A., Muñoz Sabater J., *et al.* (2023).
442 ERA5 hourly data on single levels from 1940 to present
- 443 Hetem R.S., Fuller A., Maloney S.K. & Mitchell D. (2014). Responses of large mammals to
444 climate change. *Temperature* **1**, 115–127. <https://doi.org/10.4161/temp.29651>
- 445 Hijmans R.J. (2023). *Terra: Spatial data analysis*.
- 446 Hollister J., Shah T., Nowosad J., Robitaille A.L., Beck M.W. & Johnson M. (2023). *Elevatr:*
447 *Access elevation data from various APIs*.
- 448 Hou R., Chapman C.A., Jay O., Guo S., Li B. & Raubenheimer D. (2020). Cold and

- 449 hungry: Combined effects of low temperature and resource scarcity on an edge-of-range
450 temperate primate, the golden snub-nose monkey. *Ecography* **43**, 1672–1682. <https://doi.org/10.1111/ecog.05295>
- 452 Intergovernmental Panel On Climate Change (2023). *Climate change 2021 – the physical*
453 *science basis: Working group i contribution to the sixth assessment report of the inter-*
454 *governmental panel on climate change*, 1st edn. Cambridge University Press.
- 455 Jahn M. & Seebacher F. (2022). Variations in cost of transport and their ecological conse-
456 quences: A review. *Journal of Experimental Biology* **225**, jeb243646. <https://doi.org/10.1242/jeb.243646>
- 458 Johnson D.H. (1980). The comparison of usage and availability measurements for evaluating
459 resource preference. *Ecology* **61**, 65–71. <https://doi.org/10.2307/1937156>
- 460 Kacelnik A., Krebs J.R. & Bernstein C. (1992). The ideal free distribution and predator-prey
461 populations. *Trends in Ecology & Evolution* **7**, 50–55. [https://doi.org/10.1016/0169-5347\(92\)90106-L](https://doi.org/10.1016/0169-5347(92)90106-L)
- 463 Kays R., Davidson S.C., Berger M., Bohrer G., Fiedler W., Flack A., et al. (2022). The
464 movebank system for studying global animal movement and demography. *Methods in*
465 *Ecology and Evolution* **13**, 419–431. <https://doi.org/10.1111/2041-210X.13767>
- 466 Kutz S. & Tomaselli M. (2019). “Two-eyed seeing” supports wildlife health. *Science* **364**,
467 1135–1137. <https://doi.org/10.1126/science.aau6170>
- 468 Leclerc M., Leblond M., Le Corre M., Dussault C. & Côté S.D. (2021). Determinants of
469 migration trajectory and movement rate in a long-distance terrestrial mammal. *Journal*
470 *of Mammalogy* **102**, 1342–1352. <https://doi.org/10.1093/jmammal/gyab081>
- 471 Levins R.A. (1974). *Evolution in changing environments: Some theoretical explorations*, 3.
472 printing. Princeton Univ. Press, Princeton, NJ.
- 473 Li P., Yang J., Islam M.A. & Ren S. (2023). Making AI less ”thirsty”: Uncovering and
474 addressing the secret water footprint of AI models
- 475 Li Z. & Wood S.N. (2020). Faster model matrix crossproducts for large generalized linear

- 476 models with discretized covariates. *Statistics and Computing* **30**, 19–25. <https://doi.org/10.1007/s11222-019-09864-2>
- 477
- 478 Luccioni A.S., Viguer S. & Ligozat A.-L. (2024). Estimating the carbon footprint of
479 BLOOM, a 176B parameter language model. *J. Mach. Learn. Res.* **24**
- 480 Martinez-Garcia R., Fleming C.H., Seppelt R., Fagan W.F. & Calabrese J.M. (2020). How
481 range residency and long-range perception change encounter rates. *Journal of Theoretical
482 Biology* **498**, 110267. <https://doi.org/10.1016/j.jtbi.2020.110267>
- 483 Matthiopoulos J. (2022). Defining, estimating, and understanding the fundamental niches
484 of complex animals in heterogeneous environments. *Ecological Monographs* **92**, e1545.
485 <https://doi.org/10.1002/ecm.1545>
- 486 McCain C.M. (2019). Assessing the risks to united states and canadian mammals caused
487 by climate change using a trait-mediated model. *Journal of Mammalogy*, gyz155. <https://doi.org/10.1093/jmammal/gyz155>
- 488
- 489 McElreath R. (2016). *Statistical rethinking: A bayesian course with examples in r and stan.*
490 CRC Press/Taylor & Francis Group, Boca Raton.
- 491 Melin M., Matala J., Mehtätalo L., Pusenius J. & Packalen T. (2023). The effect of snow
492 depth on movement rates of GPS-collared moose. *European Journal of Wildlife Research*
493 **69**, 21. <https://doi.org/10.1007/s10344-023-01650-w>
- 494 Merkle J.A., Monteith K.L., Aikens E.O., Hayes M.M., Hersey K.R., Middleton A.D., *et al.*
495 (2016). Large herbivores surf waves of green-up during spring. *Proceedings of the Royal
496 Society B: Biological Sciences* **283**, 20160456. <https://doi.org/10.1098/rspb.2016.0456>
- 497 Mezzini S., Fleming C.H., Medici E.P. & Noonan M.J. (2024). How resource abundance and
498 stochasticity affect organisms' range sizes
- 499 Montgomery R.A., Redilla K.M., Moll R.J., Van Moorter B., Rolandsen C.M., Millspaugh
500 J.J., *et al.* (2019). Movement modeling reveals the complex nature of the response of
501 moose to ambient temperatures during summer. *Journal of Mammalogy* **100**, 169–177.
502 <https://doi.org/10.1093/jmammal/gyy185>

- 503 Mota-Rojas D., Titto C.G., Orihuela A., Martínez-Burnes J., Gómez-Prado J., Torres-Bernal
504 F., *et al.* (2021). Physiological and behavioral mechanisms of thermoregulation in mam-
505 mals. *Animals* **11**, 1733. <https://doi.org/10.3390/ani11061733>
- 506 Nathan R., Getz W.M., Revilla E., Holyoak M., Kadmon R., Saltz D., *et al.* (2008). A
507 movement ecology paradigm for unifying organismal movement research. *Proceedings
508 of the National Academy of Sciences* **105**, 19052–19059. [https://doi.org/10.1073/pnas.0800375105](https://doi.org/10.1073/pnas.
509 0800375105)
- 510 Noonan M.J., Fleming C.H., Akre T.S., Drescher-Lehman J., Gurarie E., Harrison A.-L.,
511 *et al.* (2019a). Scale-insensitive estimation of speed and distance traveled from animal
512 tracking data. *Movement Ecology* **7**, 35. <https://doi.org/10.1186/s40462-019-0177-1>
- 513 Noonan M.J., Tucker M.A., Fleming C.H., Akre T.S., Alberts S.C., Ali A.H., *et al.* (2019b).
514 A comprehensive analysis of autocorrelation and bias in home range estimation. *Ecolog-
515 ical Monographs* **89**, e01344. <https://doi.org/10.1002/ecm.1344>
- 516 Pease B.S. (2024). Ecological scales of effect vary across space and time. *Ecography* **2024**,
517 e07163. <https://doi.org/10.1111/ecog.07163>
- 518 Pedersen E.J., Miller D.L., Simpson G.L. & Ross N. (2019). Hierarchical generalized additive
519 models in ecology: An introduction with mgcv. *PeerJ* **7**, e6876. [https://doi.org/10.7717/peerj.6876](https://doi.org/10.7717/
520 peerj.6876)
- 521 Peterson A.N., Soto A.P. & McHenry M.J. (2021). Pursuit and evasion strategies in the
522 predator-prey interactions of fishes. *Integrative and Comparative Biology* **61**, 668–680.
523 <https://doi.org/10.1093/icb/icab116>
- 524 Polazzo F., Limberger R., Pennekamp F., Ross S.R.P.-J., Simpson G.L. & Petchey O.L.
525 (2024). Measuring the response diversity of ecological communities experiencing multi-
526 farious environmental change. *Global Change Biology* **30**, e17594. [https://doi.org/10.1111/gcb.17594](https://doi.org/10.
527 1111/gcb.17594)
- 528 R Core Team (2024). *R: A language and environment for statistical computing*. R Foundation
529 for Statistical Computing, Vienna, Austria.

- 530 Riahi K., Vuuren D.P. van, Kriegler E., Edmonds J., O'Neill B.C., Fujimori S., *et al.* (2017).
531 The shared socioeconomic pathways and their energy, land use, and greenhouse gas
532 emissions implications: An overview. *Global Environmental Change* **42**, 153–168. <https://doi.org/10.1016/j.gloenvcha.2016.05.009>
- 533
- 534 Rigby R.A. & Stasinopoulos D.M. (2005). Generalized additive models for location, scale
535 and shape (with discussion). *Journal of the Royal Statistical Society: Series C (Applied
536 Statistics)* **54**, 507–554. <https://doi.org/10.1111/j.1467-9876.2005.00510.x>
- 537 Sawyer H., Kauffman M.J., Nielson R.M. & Horne J.S. (2009). Identifying and prioritizing
538 ungulate migration routes for landscape-level conservation. *Ecological Applications* **19**,
539 2016–2025. <https://doi.org/10.1890/08-2034.1>
- 540 Sawyer H., Merkle J.A., Middleton A.D., Dwinnell S.P.H. & Monteith K.L. (2019). Migratory
541 plasticity is not ubiquitous among large herbivores. *Journal of Animal Ecology* **88**,
542 450–460. <https://doi.org/10.1111/1365-2656.12926>
- 543 Schmidt N.M., Grøndahl C., Evans A.L., Desforges J.-P., Blake J., Hansen L.H., *et al.*
544 (2020). On the interplay between hypothermia and reproduction in a high arctic ungu-
545 late. *Scientific Reports* **10**, 1514. <https://doi.org/10.1038/s41598-020-58298-8>
- 546 Sherwood S.C. & Huber M. (2010). An adaptability limit to climate change due to heat
547 stress. *Proceedings of the National Academy of Sciences* **107**, 9552–9555. <https://doi.org/10.1073/pnas.0913352107>
- 548
- 549 Sih A., Ferrari M.C.O. & Harris D.J. (2011). Evolution and behavioural responses to human-
550 induced rapid environmental change: Behaviour and evolution. *Evolutionary Applica-
551 tions* **4**, 367–387. <https://doi.org/10.1111/j.1752-4571.2010.00166.x>
- 552 Stasinopoulos M.D. & Rigby R.A. (2007). Generalized additive models for location scale
553 and shape (GAMLSS) in r. *Journal of Statistical Software* **23**
- 554 Tan M., Zhang S., Stevens M., Li D. & Tan E.J. (2024). Antipredator defences in motion:
555 Animals reduce predation risks by concealing or misleading motion signals. *Biological
556 Reviews* **99**, 778–796. <https://doi.org/10.1111/brv.13044>

- 557 Taylor C.R., Heglund N.C. & Maloij G.M.O. (1982). Energetics and mechanics of terrestrial
558 locomotion. I. Metabolic energy consumption as a function of speed and body size in
559 birds and mammals. *Journal of Experimental Biology* **97**, 1–21. <https://doi.org/10.1242/jeb.97.1.1>
- 560
- 561 Tuanmu M. & Jetz W. (2014). A global 1-km consensus land-cover product for biodiversity
562 and ecosystem modelling. *Global Ecology and Biogeography* **23**, 1031–1045. <https://doi.org/10.1111/geb.12182>
- 563
- 564 Verzuh T.L., Rogers S.A., Mathewson P.D., May A., Porter W.P., Class C., *et al.* (2023).
565 Behavioural responses of a large, heat-sensitive mammal to climatic variation at multiple
566 spatial scales. *Journal of Animal Ecology* **92**, 619–634. <https://doi.org/10.1111/1365-2656.13873>
- 567
- 568 Weststrate D.K., Chhen A., Mezzini S., Safford K. & Noonan M.J. (2024). How climate
569 change and population growth will shape attendance and human-wildlife interactions at
570 british columbia parks. *Journal of Sustainable Tourism*, 1–15. <https://doi.org/10.1080/09669582.2024.2331228>
- 571
- 572 Williams J.E. & Blois J.L. (2018). Range shifts in response to past and future climate change:
573 Can climate velocities and species' dispersal capabilities explain variation in mammalian
574 range shifts? *Journal of Biogeography* **45**, 2175–2189. <https://doi.org/10.1111/jbi.13395>
- 575
- 576 Wilson R.S., Franklin C.E., Davison W. & Kraft P. (2001). Stenotherms at sub-zero tem-
577 peratures: Thermal dependence of swimming performance in antarctic fish. *Journal of
578 Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology* **171**,
263–269. <https://doi.org/10.1007/s003600000172>
- 579
- 580 Winter V.A., Smith B.J., Berger D.J., Hart R.B., Huang J., Manlove K., *et al.* (2024).
581 Forecasting animal distribution through individual habitat selection: Insights for pop-
582 ulation inference and transferable predictions. *Ecography*, e07225. <https://doi.org/10.1111/ecog.07225>
- 583
- 584 Wood S.N. (2017). *Generalized additive models: An introduction with r*, Second edition.

- 584 CRC Press/Taylor & Francis Group, Boca Raton.
- 585 Wood S.N., Goude Y. & Shaw S. (2015). Generalized additive models for large data sets.
- 586 *Journal of the Royal Statistical Society: Series C (Applied Statistics)* **64**, 139–155. <https://doi.org/10.1111/rssc.12068>
- 587
- 588 Wood S.N., Li Z., Shaddick G. & Augustin N.H. (2017). Generalized additive models for
- 589 gigadata: Modeling the u.k. Black smoke network daily data. *Journal of the American*
- 590 *Statistical Association* **112**, 1199–1210. <https://doi.org/10.1080/01621459.2016.1195744>
- 591 Woo-Durand C., Matte J.-M., Cuddihy G., McGourdji C.L., Venter O. & Grant J.W.A.
- 592 (2020). Increasing importance of climate change and other threats to at-risk species in
- 593 canada. *Environmental Reviews* **28**, 449–456. <https://doi.org/10.1139/er-2020-0032>
- 594 Xu W., Barker K., Shawler A., Van Scyoc A., Smith J.A., Mueller T., *et al.* (2021).
- 595 The plasticity of ungulate migration in a changing world. *Ecology* **102**, e03293. <https://doi.org/10.1002/ecy.3293>
- 596
- 597 Zurowski M. (2023). *The summer canada burned: The wildfire season that shocked the world.*
- 598 Postmedia / Greystone Books, Vancouver.