

The heat is on: Rising temperatures alter when, how, and where
large terrestrial mammals move

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Abstract

Recent widespread warming has caused many terrestrial mammals to change when, how, and where they move, with cascading effects on fitness, habitat selection, and community structure. Previous studies have quantitatively estimated the effects of temperature on mammalian movement behaviour, but few have estimated the effects of future climate change. Consequently, it is still unclear how mammals will adapt their movement behavior 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 western Canada between 1998 and 2023. We show that temperature is a strong determinant of when, how, and where mammals move, and we predict that climate change will impact mammals' movement rates and habitat selection as temperatures warm throughout the 21st century. We found the effects of temperature on movement rates varied across species, so we suggest that species' estimated responses be interpreted holistically when making inferences about how climate change will impact ecological communities. In contrast, habitat selection strength decreased for all species within their observed ranges, suggesting that all six species may shift their range in the coming decades. As climate change exposes mammals to novel environmental conditions, predicting changes in animal behavior and community structure will become crucial for effective and proactive conservation. We thus conclude by providing suggestions for conservation and future research, with particular attention to the study design, statistical modeling, and forecasting. We provide detailed R code and appendices so that other researchers can implement our methods on their own datasets.

¹ 1 Introduction

² For most animals, movement is a rapid and low-cost response to a variety of stimuli (Nathan
³ *et al.*, 2008). Animals move to maximize resource availability (e.g., food, water, shelter, see:
⁴ Charnov, 1976; Kacelnik *et al.*, 1992), optimize habitat use (Winter *et al.*, 2024), and escape
⁵ predation (Peterson *et al.*, 2021; Bartashevich *et al.*, 2024; Tan *et al.*, 2024). However,
⁶ ambient temperature affects mammals' movement rates by altering the energetic cost of
⁷ movement (McNab, 1970; Taylor *et al.*, 1982; Brown *et al.*, 2004; Fuller *et al.*, 2016; Jahn
⁸ & Seebacher, 2022) and the risk of overheating (Hetem *et al.*, 2014; Dyer *et al.*, 2023).
⁹ Animals may search for a short-term buffer from extreme heat or cold via thermal refugia
¹⁰ (Hannah *et al.*, 2014; Elmore *et al.*, 2017; Attias *et al.*, 2018; Arechavala-Lopez *et al.*, 2019;
¹¹ Gulland *et al.*, 2022), which may even be preferred over forage abundance (e.g., Hall *et al.*,
¹² 2016). Additionally, temperature also has indirect effects on movement through other drivers
¹³ of movement behaviour, such as trophic interactions (Hegel *et al.*, 2010), snow depth and
¹⁴ density (Montgomery *et al.*, 2019; Leclerc *et al.*, 2021; Melin *et al.*, 2023), and the frequency
¹⁵ and intensity of extreme events (Bunnell *et al.*, 2011; Zhang *et al.*, 2023), including forest
¹⁶ fires, droughts, and novel phenology (Bunnell *et al.*, 2011; Duncan *et al.*, 2012; Merkle *et*
¹⁷ *al.*, 2016; Slatyer *et al.*, 2022; Zurowski, 2023). Changes in temperature thus affects how
¹⁸ animals move (e.g., movement frequency and speed – their movement behaviour: Nathan *et*
¹⁹ *al.*, 2008; Dyer *et al.*, 2023) and where they move to (i.e., their habitat selection: Merkle *et*
²⁰ *al.*, 2016; Alston *et al.*, 2020; Giroux *et al.*, 2023).

²¹ By impacting animal movement behavior, temperature also affects the consequences of
²² movement, such as encounter rates with resources (Mezzini *et al.*, 2025), other animals
²³ (Martinez-Garcia *et al.*, 2020), and humans (Weststrate *et al.*, 2024), and these changes are
²⁴ exacerbated at extreme temperatures (Wilson *et al.*, 2001; Berger *et al.*, 2018; Giroux *et al.*,
²⁵ 2023). But what counts as “extreme” varies across species: Species that experience narrow
²⁶ temperature ranges tend to be more sensitive to changes (e.g., giant anteaters, *Myrmecophaga*

tridactyla: Giroux *et al.*, 2023), while thermal generalists can adapt more easily to change (Levins, 1974; Botero *et al.*, 2015; Dupont *et al.*, 2024). However, generalists' greater adaptability is tested when they are subject to changes that are more severe (McCain, 2019), affect many factors (e.g., temperature, phenology, and resource availability: Polazzo *et al.*, 2024), or are too rapid to respond within the span of a lifetime or a few generations (Levins, 1974; Fuller *et al.*, 2016; Xu *et al.*, 2021).

In the last 200 years, many ecosystems experienced widespread warming that resulted in milder and shorter winters, hotter and longer summers, and a greater risk of extremely high temperatures (IPCC, 2023). Over the next 100 years, these changes are expected to worsen and continue to impact mammals' fitness, movement behaviour, and habitat selection as animals cope with growing heat stress (Deb *et al.*, 2020; Woo-Durand *et al.*, 2020) and more frequent and intense extreme events (Bunnell *et al.*, 2011), along with increasing anthropogenic pressure (Sawyer *et al.*, 2009; Sih *et al.*, 2011; Weststrate *et al.*, 2024). Consequently, it remains unclear how or whether species will be able to respond to climate change in the current century (Deb *et al.*, 2020; Woo-Durand *et al.*, 2020; Verzuh *et al.*, 2023), especially when populations fail to adapt to changes (Botero *et al.*, 2015; Sawyer *et al.*, 2019) or are physiologically incapable to do so (Sherwood & Huber, 2010; Williams & Blois, 2018). Uncertainty in future conditions and their consequences on ecosystems present a need for a comprehensive understanding of (1) the direct effects of temperature on animal movement behaviour and (2) the implications such changes and uncertainty will have on populations and species' adaptability and resiliency, as well as overall community structure. Recent work has documented the effects of climate change on mammals' ranges (Leclerc *et al.*, 2021), movement behaviour (Melin *et al.*, 2023), thermoregulation (Mota-Rojas *et al.*, 2021), and trait-based responses (e.g., body size, activity time, and elevational and latitudinal distribution McCain, 2019). However, it is still unclear how mammals will adapt their small-scale movement and habitat selection to changes in temperature during the 21st century (IPCC, 2023; but see Hetem *et al.*, 2014; Winter *et al.*, 2024).

54 Understanding the direct and indirect impacts of temperature on mammalian movement
55 is essential for decision makers to respond to change in a proactive manner (Sawyer *et al.*,
56 2009; McCain, 2019). The Canadian province of British Columbia is currently experiencing
57 rapid widespread warming (Turner & Clifton, 2009; Dierauer *et al.*, 2021), phenological shifts
58 (Basu *et al.*, 2024; Tysor, 2025), and more frequent and intense extreme events (Zhang *et*
59 *al.*, 2023), including forest fires (Zurowski, 2023). As we approach the deadline for the
60 “30 by 30” conservation initiative, a global effort to conserve 30% of the world’s lands and
61 oceans by 2030 (Convention on Biological Diversity, 2022), decision makers must understand
62 which areas will be of greatest value for maximizing the project’s effectiveness. Predicting
63 how climate change will affect how, when, and where animals will move is necessary for
64 identifying landscape dynamics and value will evolve throughout the century. Failing to
65 understand how changes in temperature will affect mammalian movement behaviour and
66 habitat selection will hinder our ability to respond to the current climate crisis and make
67 decisions that are viable in the long term.

68 This paper provides a framework for quantifying the effects of proximal air temperature
69 on animal movement using quantitative methods that are flexible and statistically robust.
70 We present results for six large-bodied terrestrial mammal species in western Canada (wolves:
71 *Canis lupus*, elk: *Cervus canadensis*, mountain goats: *Oreamnos americanus*, cougars: *Puma*
72 *concolor*, boreal and southern mountain caribou: *Rangifer tarandus*, and grizzly bears: *Urs-*
73 *sus arctos horribilis*; Table 1). Using over 25 years of telemetry data throughout a large
74 spatial range of British Columbia and hourly air temperature data, we estimate how these
75 mammals altered their probability of movement, speed when moving, and habitat selec-
76 tion in response to temperature. We then pair the estimated responses with climate change
77 projections to forecast the species’ movement during the 21st century under different climate-
78 change scenarios (referred to as Shared Socioeconomic Pathways, SSP, Riahi *et al.*, 2017).
79 We disentangle the direct and indirect effects of temperature on the movement behaviour
80 of terrestrial mammals and discuss the consequences of these changes at the individual,

81 population, and community levels.

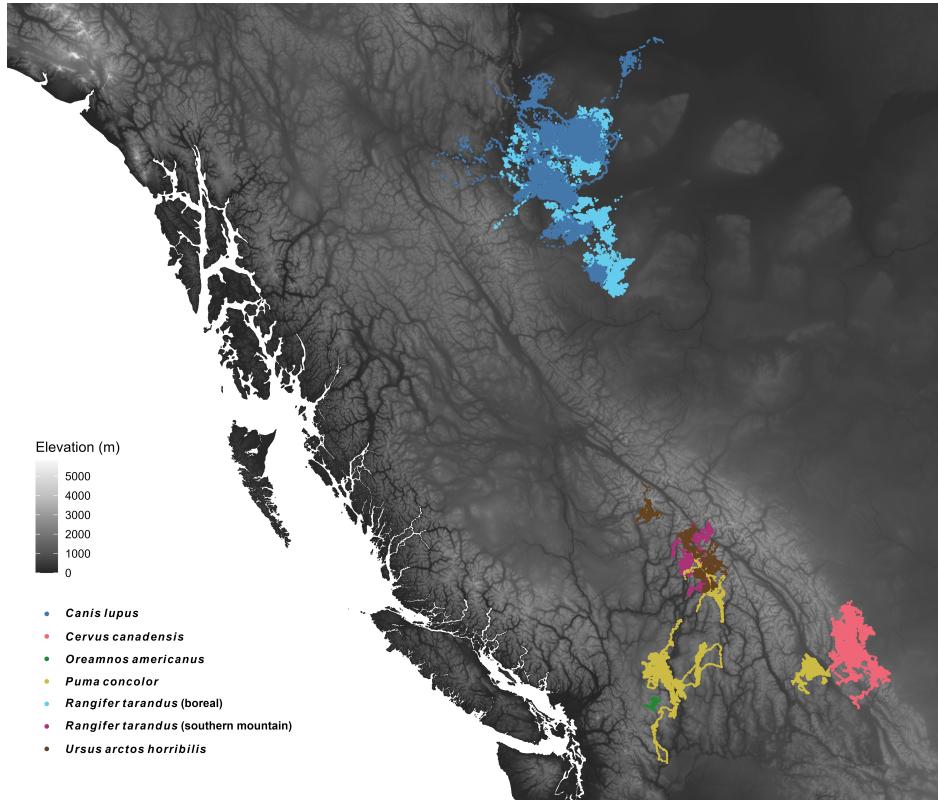


Figure 1: GPS telemetry data for the six species in this study (dots) over a digital elevation model for the study area.

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 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
<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

82 **2 Methods**

83 **2.1 Datasets used**

84 This study leverages four main datasets: (1) a multi-species collection of GPS telemetry
85 data (Fig. 1); (2) historical hourly reanalyzed air temperature from the ERA5 dataset from
86 the European Center for Medium-range Weather Forecasting; (3) resource rasters of percent
87 forest cover, elevation, and distance from water; and (4) climate change projections under
88 four Shared Socioeconomic Pathways (SSPs, see Riahi *et al.*, 2017). While we acknowledge
89 that forest type, structure, and age are important variables, we do not include such variables
90 in this study for the sake of parsimony and comparability across species. We detail the data
91 sources and analyses in the sections below.

92 **2.1.1 GPS telemetry data**

93 Elk (*Cervus canadensis*) data from Ciuti *et al.* (2012) were downloaded from Movebank
94 (study name: Elk in southwestern Alberta, see Kays *et al.*, 2022), while boreal caribou
95 (*Rangifer tarandus*) and wolf (*Canis lupus*) telemtries were acquired via a public British
96 Columbia Oil and Gas Research and Innovation Society repository (<https://www.bcogris.ca/projects/boreal-caribou-telemetry-data>). **MISSING INFO ON OTHER TELEME-**
97 **TRY DATA.** From the full set of telemetry data, a total of 2396 GPS locations (0.16%,
99 including collar calibration data) were removed using diagnostic plots of (1) distance from
100 the median location, (2) straight-line displacement between locations, (3) turning angle, and
101 (4) time interval between consecutive points. Particular attention was paid to points with
102 large turning angles ($\gtrapprox 170^\circ$) and excessively high straight-line displacement, especially if
103 antecedent and subsequent points indicated stationary behaviour (Appendix A).

104 **2.1.2 Historical temperature data and temperature projections**

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

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

126 We simulated hourly variation in future weather by assuming hourly temperature fol-
127 lowed a normal distribution with mean specified by the monthly `climatenetR` climate pro-
128 jections and variance as specified by the Gamma GAMLS. For each month within each year
129 from 2020 to 2100, we simulated hourly weather by including temperatures from the 0.1 to
130 the 0.9 quantile by increments of 0.1, and we weighted each quantile proportionally to the

131 (normalized) Gaussian probability density for each quantile.

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 needle-leaf 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, Fleming *et al.*, 2014; Noonan *et al.*, 2019a).
150 The 18 animals with insufficiently fine sampling to support movement models with finite
151 speed (Noonan *et al.*, 2019a) were for one mountain goat, 15 boreal caribou, and 2 southern
152 mountain caribou (Table 1).

153 Since 'ctmm's movement models assume stochastic but non-zero speeds (i.e., a sin-
154 gle, stochastic moving state), data-informed speeds needed to be corrected so that the
155 minimum instantaneous speed could be 0. We performed this correction by subtracting

156 each model's mean speed while assuming speeds were χ^2 -distributed. The function we
157 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
158 small, non-zero speeds, we determined whether an animal was moving or not using a k -means
159 algorithm with 2 clusters for each species' detrended speeds. When the algorithm clearly
160 failed to discriminate between states, we estimated the split point using the inflection points
161 in histograms of the detrended speeds (Fig. B1).
162

163 **2.3 Estimating the effects of temperature on mammals' movement**

164 The following sections detail the statistical framework and modelling we used to estimate
165 the effect on temperature on mammals' movement. To assess the importance of including
166 temperature as an explicit covariate (rather than including its effects with time of day and
167 day of year), we fit models with and without smooth effects of temperature and compared
168 the fits of the two sets of models.

169 **2.3.1 Disentangling direct and indirect effects**

170 In this study, we separate the effects of temperature on mammalian movement into direct
171 and indirect effects. We call "direct" all effects that impact movement behavior causally
172 without first impacting another variable (Fig. 2). For example, in Fig. 2A, whether a
173 grizzly bear is moving in a given moment directly depends on time of day and day of year,
174 since it will not be moving when sleeping or hibernating. However, time of day and day of
175 year also impact its movement behavior indirectly because its sensitivity to temperature will
176 also depend on time of day and day of year. Thus, both time of day and day of year also
177 impact movement frequency indirectly by altering the effect of temperature on movement
178 frequency. Failing to disentangle the effects of these three variables will lead to incorrect and
179 likely confusing estimates for the causal effect of temperature on movement behavior, since
180 causal and non-causal relationships would be indistinguishable (McElreath, 2020).

181 Indirect effects of temperature also include all effects that can be controlled by altering
 182 an animal's habitat (its geographic space *sensu* Matthiopoulos, 2022). For example, in Fig.
 183 2B, an increase in temperature may push an animal to prefer higher forest cover in search of
 184 shade, and conservationists can mitigate these indirect effects of temperature by increasing
 185 the availability of forested areas, since the effect of temperature on movement is conditional
 186 on forest cover availability. In contrast, the animal may avoid moving if temperatures are
 187 above 35°C, irrespective of its geographic and environmental space (*sensu* Matthiopoulos,
 188 2022). In this case, it is not possible to mitigate the effects of temperature on movement
 189 behaviour (other than changing temperature directly).

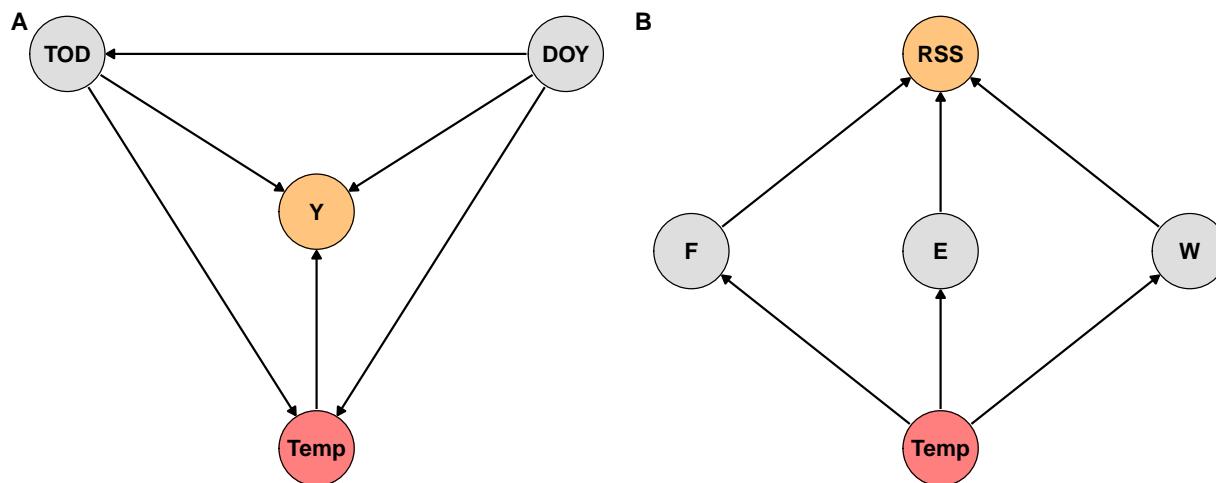


Figure 2: Directed Acyclical Graphs (DAGs) assumed for inferring the causal effects of temperature (Temp) on movement behavior. (A) DAG for the probability of moving, speed when moving, or distance traveled (Y) while accounting for the effects of time of day (TOD), day of year (DOY), and their interaction effects. Temperature directly affects Y, but the effects of temperature depend on the time of day and season. Time of day and day of year also affect Y directly, but the effect of time of day changes throughout the year due to changes in day length and seasonality. (B) DAG for Relative Selection Strength (RSS) for percent forest cover (F), elevation (E), and distance from water (W). The RSS for of a given habitat depends on all three resources, and the selection for each resource is independent of the other two resources and dependent on temperature.

190 2.3.2 Effects of temperature on movement rates

191 We estimated the effects of temperature (°C) on mammals' instantaneous movement state
 192 (moving or not) and speed when moving using two Hierarchical Generalized Additive Models
 193 (HGAMs, see Pedersen *et al.*, 2019 and the code chunk below) with the `mgcv` package for R
 194 (version 1.9-1, Wood, 2017). The first HGAM estimated the probability that an animal was
 195 moving, $P(M)$, with a binomial family of distributions and logit link function. The response

variable moving was coded as 1 if moving and 0 if not. The second HGAM estimated an animal's speed when moving (`speed`) with a gamma family of distributions and log link function.

The HGAMs included random intercepts for each animal (`s(animal, bs = 're')`), fixed-effect intercepts for each species (`species`), and species-level by smooths (`s(..., by = species)`), which allowed each species' term to be estimated independent of other species (see model I in Figure 4 of Pedersen *et al.*, 2019). The by smooths accounted for trends in time of day (in Pacific Daylight Time; `tod_pdt`), day of year (`doy`), and temperature (`temp_c`). The models also had three tensor product interaction terms (`ti()`) by 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). Finally, smooth terms of log-transformed hours between GPS locations (`dt`) accounted for irregular sampling rates. A global term of `log(dt)` accounted for the overall effect of sampling interval, while a factor-smooth interaction term (`s(log(dt), species, bs = 'fs')`) allowed for species-level deviations from the global term while assuming a common smoothness parameter across species (see model GS in Figure 4 of Pedersen *et al.*, 2019).

The HGAMs accounted for the cyclicity of time of day and day of year using cyclic cubic splines (`bs = 'cc'`, see p. 202 of Wood, 2017). We fit the models with fast Restricted Maximum Likelihood ('`fREML`') and discretized covariates (`discrete = TRUE`) to optimize computational efficiency with no appreciable losses to model performance (Appendix B; Wood *et al.*, 2015, 2017; Li & Wood, 2020). Together, the binomial HGAM and the gamma HGAM inform us on an animal's long-term average speed, since it is the product of the probability of moving and its average speed when moving.

```

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)))

```

2.3.3 Effects of temperature on habitat selection

We estimated the effects of temperature on each species' selection for percent forest cover (`forest_perc`), elevation (`elevation_m`), and distance from water (`dist_water_m`) by fitting a Hierarchical Resource Selection Function for each species using an HGAM with a Poisson family of distributions and log link function (Appendix B; Aarts *et al.*, 2008). After removing non-resident individuals (Table B1), we accounted for the spatiotemporal autocorrelation in the telemetry locations by weighting each point based on the telemetry's Autocorrelated Kernel Density Estimate (Fleming & Calabrese, 2017; Noonan *et al.*, 2019b) to produce estimates of second- and third-order habitat selection (Johnson, 1980). While we recognize there are other important drivers of habitat selection (e.g., forest age, forest type, terrain ruggedness, prey availability), we decided to only use these three proxies to produce results that are easily comparable across species. Each species' model had the same

233 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)
```

234 Smooth effects of percent forest cover, elevation, and distance to water accounted for
235 the species-level average selection strength for each resource. A random effect for each in-
236 dividual animal (`s(animal, bs = 're')`) corrected for uneven sampling across individuals,
237 while factor smooth interaction terms (`bs = 'fs'`) accounted for individual-level resource
238 selection (i.e., individual-level deviations from the species-level average). Tensor interaction
239 product terms (`ti()`) of the three resources and temperature estimated the change in re-
240 source selection at different temperatures. Finally, we included marginal smooth terms of
241 temperature to account for species- and individual-level sampling biases over temperature
242 (e.g., sampling more during warm periods). Detections were weighted proportionally to their
243 degree of independence from other temporally proximate detections (`weights = weight` –
244 Appendix B; Alston *et al.*, 2022), while quadrature points had a weight of 1. Quadrature
245 points were obtained using all raster cells in the 99.9% AKDE percentile. The number of
246 quadrature locations greatly outnumbered the number of observed locations (Fig. B12),
247 especially after accounting for weighting based on the degree of autocorrelation and the
248 number of home range crossings (Fig. B13).

²⁴⁹ **3 Results**

²⁵⁰ Overall, 2.6% of GPS locations had temperatures lower than -20°C , while 6.5% had temper-
²⁵¹ atures above 20°C , and temperature ranges differed across species (Table 2, Fig. B2). At 0°C ,
²⁵² species differed in overall mean probabilities of movement (range: 0.05 – 0.31), mean speed
²⁵³ when moving (range: 0.42 – 2.67 km/h), and mean distance traveled (i.e., $P(M) \times \mathbb{E}(S)$,
²⁵⁴ range: 0.04 – 0.61 km/h; Table 3). Grizzly bears tended to move least often ($P(M) \approx 0.05$),
²⁵⁵ while wolves and cougars moved most often ($P(M) \geq 0.22$). When moving, mountain goats
²⁵⁶ and southern mountain caribou moved the slowest ($\mathbb{E}(S|M) \approx 0.43$ km/h), while wolves
²⁵⁷ had the highest mean speed when moving ($\mathbb{E}(S|M) \approx 2.64$ km/h). Consequently, wolves
²⁵⁸ traveled, on average, 0.6 km/h – 2.5 to 16.7 times further than other mammals at 0°C .

Table 2: Percentage of observed GPS locations (after data cleaning) with temperatures below -20°C or above 20°C .

Species	T < -20°C	T > $+20^{\circ}\text{C}$
Canis lupus	1.7 %	13.0 %
Cervus canadensis	2.4 %	4.9 %
Oreamnos americanus	0.7 %	2.8 %
Puma concolor	0.7 %	6.9 %
Rangifer tarandus (boreal)	6.8 %	7.9 %
Rangifer tarandus (s. mountain)	1.3 %	3.4 %
Ursus arctos horribilis	0.0 %	8.4 %
Total	2.6 %	6.5 %

Table 3: Mean probability of movement ($P(M)$), speed ($\mathbb{E}(S)$, km/h, assuming constant movement), and distance travelled ($P(M) \times \mathbb{E}(S) = \mathbb{E}(D)$, km/h) as estimated by models without and with temperature ($\mathbb{E}(\dots|T)$), after post-stratifying 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

Near 0°C , wolves selected for dense forest cover ($\gtrapprox 50\%$), elevations near 1 km, and distances from water < 10 km; elk selected for forest cover near 50%, elevations between 1 and 2 km, and distances from water of 5-15 km; mountain goats selected for sparse (< 50%) forest cover, elevations between 1 and 2 km; cougars selected for dense forest cover, an elevation of ~ 1 km, and distances from water < 10 km; boreal caribou selected for intermediate to dense 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.

There was relatively strong agreement between models with and without temperature (Figs. B3, and B14), but including temperature always resulted in better fits. All analyses of deviance showed that temperature significantly affected movement behavior (all p-values $< 2.2 \times 10^{-16}$; all $\Delta\text{AIC} \geq 342$; Table B2 and following pages in Appendix B). Accounting for temperature resulted in a simpler HRSF for mountain goats (lower model degrees of freedom) that fit the data better (lower deviance), and hence no test was necessary to show that the inclusion of temperature produced a better fit.

275 **3.1 Effects of temperature on movement rates**

276 The effects of temperature on movement rates varied in both direction and magnitude across
277 species, even after accounting for differences in daily and seasonal activity (e.g., sleeping,
278 migration, hibernation; Figs. B4-B6). Smooth interaction terms were well-behaved and
279 indicated clear shifts in activity over time of day and day of year for all species. The
280 models had good in-sample prediction (Fig. B7) and explained reasonably high proportions
281 of the deviance (79.3% for the Gamma model and 10.7% for the binomial model, which is
282 relatively high for a binomial model with binary responses: see ch. 11 of McElreath (2020)].
283 All species adapted their daily and seasonal movement behaviour to changes in temperature
284 (Fig. 3). The clearest example of this was cougars. In mid summer, they moved mostly
285 in the evening if temperatures were cool and mostly in the early morning if temperatures
286 were hot. Throughout the year, they tended to move more when it was colder, but what
287 they perceived as “colder” depended on the time of year. However, uncertainties around
288 the estimated effects were often higher at extreme temperatures due to data scarcity. All
289 species’ estimated probability of moving decreased with sampling intervals approximately
290 above 1 hour, and most species’ estimated speed when moving decreased monotonically with
291 sampling interval, although the estimated trends were highly uncertain for some species (Fig.
292 B8).

293 **3.2 Effects of temperature on habitat selection**

294 Species’ relative selection strength (RSS) was generally strongest for elevation and weak-
295 est for forest cover, but species’ RSS for resources depended on temperature (Fig. 4).
296 Changes in RSS with temperature were also strongest for elevation and generally weak-
297 est distance from water, but there were no common trends across all species for any of the
298 three resources. All species, with the exception of cougars, exhibited a clear temperature-
299 dependent shift in their preference for forest cover. At higher temperatures, wolves, mountain
300 goats, and grizzly bears became less selective for forest cover, while elk and caribou shifted

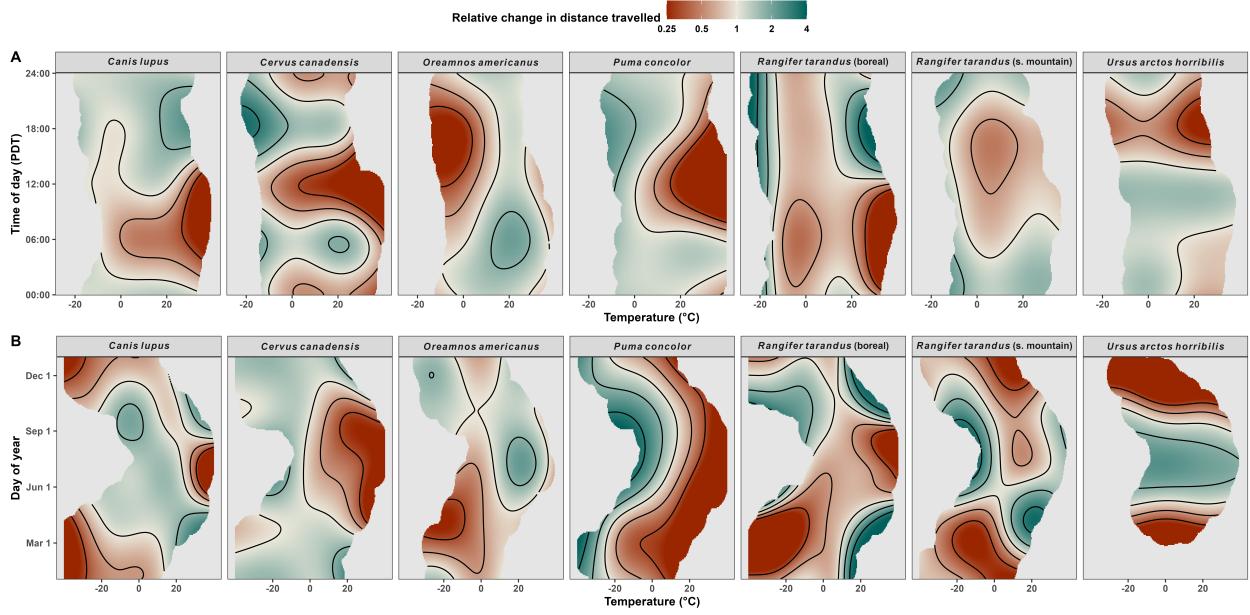


Figure 3: Temperature is a strong determinant of how far and when mammals travel. The fill indicates the estimated effects of temperature on the relative change in distance travelled (probability of moving times mean speed when moving) over time of day on June 1st (**A**) and day of year at 12:00 PDT (**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.

301 towards more intermediate forest cover without much of a change in preference width. All
302 species shifted elevationally with temperature, although boreal caribou's selection strength
303 for elevation was less sensitive to elevation. Overall, as temperatures rose, elk, mountain
304 goats, and cougars increased in elevation, while boreal wolves, southern mountain caribou,
305 and grizzly bears decreased in elevation. Most species generally remained within 5 km of
306 water, and temperature did not affect their selection strength as much as for the other two
307 resources. Again, estimated RSS values were generally most uncertain at extreme tempera-
308 tures (Fig. B15).

309 3.3 Predicted changes in movement during the 21st century

310 The predicted changes in distance traveled varied across species in both direction and magni-
311 tude, but worse climate-change SSPs always corresponded to greater absolute changes (Fig.
312 5). Additionally, species that were predicted to move less often did not necessarily have lower
313 speeds when moving, and vice versa (Figs. B9 and B10). Overall, absolute changes by 2100
314 under the best-case SSP were small (approximately 0% to +4%), while under the worst-case

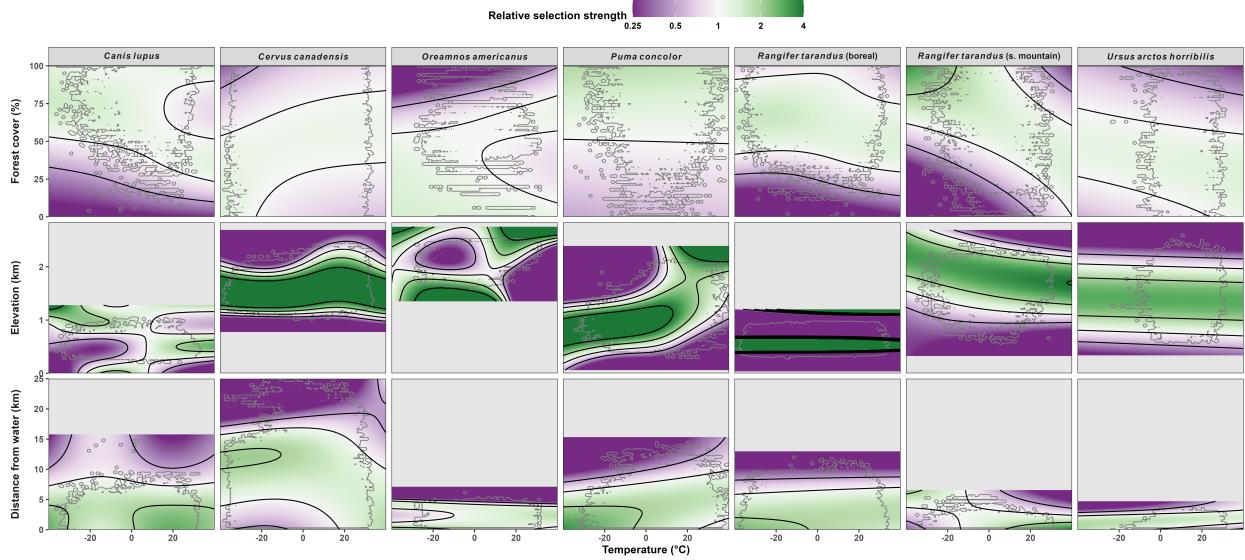


Figure 4: Temperature strongly affects mammals' habitat selection. Estimated relative selection strength (RSS) for forest cover (%), elevation (km), and distance from water (km) as a function of temperature. The grey contours indicate the extent of each species' observed data. RSS values were re-centered and capped to $2^{\pm 2}$ to improve readability.

315 SSP absolute changes ranged from ~2% (grizzly bears) to ~24% (cougars). Notably, while
 316 the models estimated that grizzly bears would move substantially less (if at all) in winter
 317 (Figs. 3, B4-B6), the models did not explicitly account for changes in hibernation phenol-
 318 ogy. Consequently, the climate change projections do not explicitly account for changes in
 319 energetic needs or physiology. Projected changes also varied spatially due to heterogeneity
 320 in projected climate change (Fig. 6). Again, absolute changes were generally greatest under
 321 worse SSPs, but the direction of change at each location also varied across SSPs (most visible
 322 in cougars).

323 Median RSS was projected to decrease over time within the each species' observed range,
 324 but changes were stronger under worse SSPs (Fig. 8). Decreases were most pronounced in
 325 the bottom fifth percentile and most severe for elk, southern mountain caribou, and mountain
 326 goats. Of all the species, only cougars showed a clear increase in RSS for areas within their
 327 current range. The change in RSS between 2025 and 2100 varied spatially for all species
 328 (Fig. 8). All species were predicted to exhibit a decrease in RSS throughout most of their
 329 observed habitats, although cougars were predicted to increase their selection for patches
 330 with higher altitude.

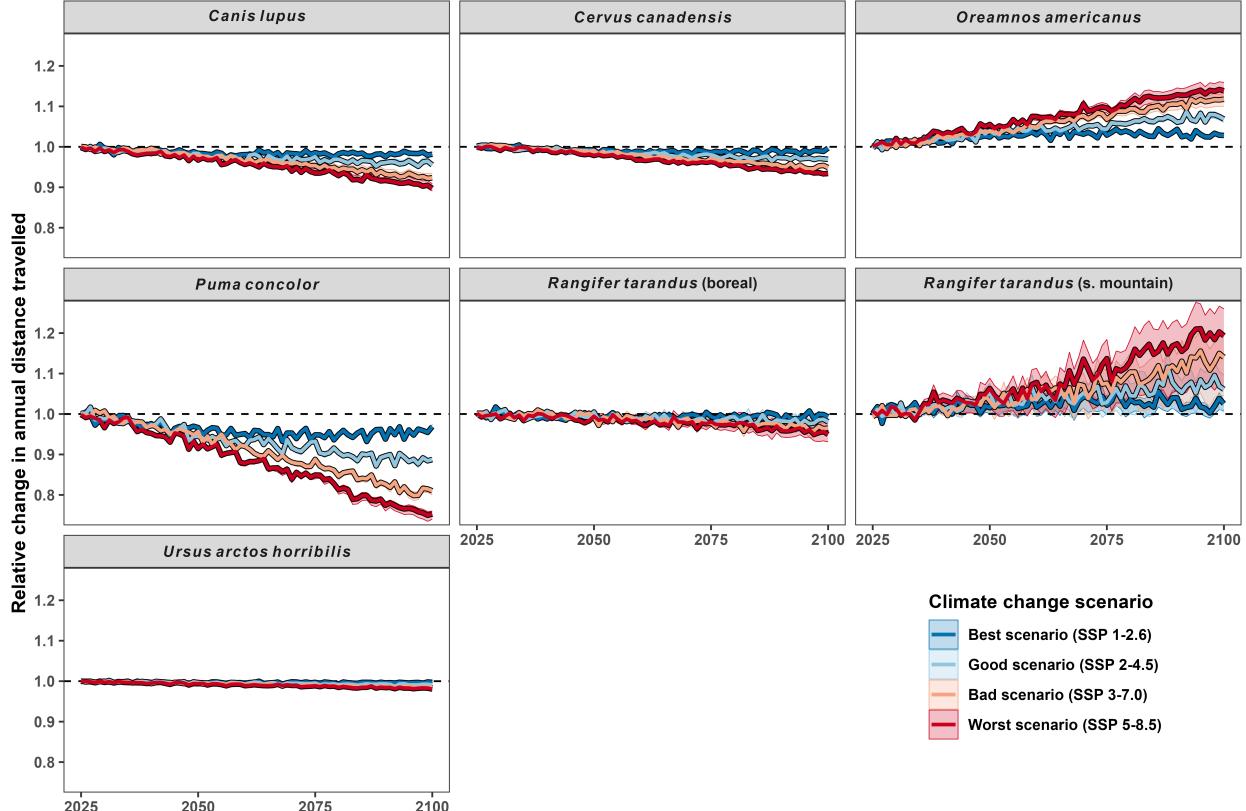


Figure 5: **The direction and magnitude of changes in movement rates due to climate change varies among species, but worse climate-change scenarios result in the greatest change.** Lines indicate the median projected change in distance travelled (probability of moving times speed when moving) due to changes in temperature within the area delimitated by the 99.9% Autocorrelated Density Kernel Estimates of space use. Shaded areas indicate the range of predicted values between the 95th and 5th percentiles. Changes are relative to the predicted mean distances travelled in 2025 across the four Shared Socioeconomic Pathways (SSPs). If the intervals are fully above the dashed line, at least 90% of the estimated means increased, relative to the each pixel's average of the four climate SSPs in 2025. Similar conclusions can be drawn regarding a decrease if the ribbons are below the dashed line. The projections only account for changes in movement behaviour (i.e., movement frequency and speed) and ignore changes in physiology or movement costs.

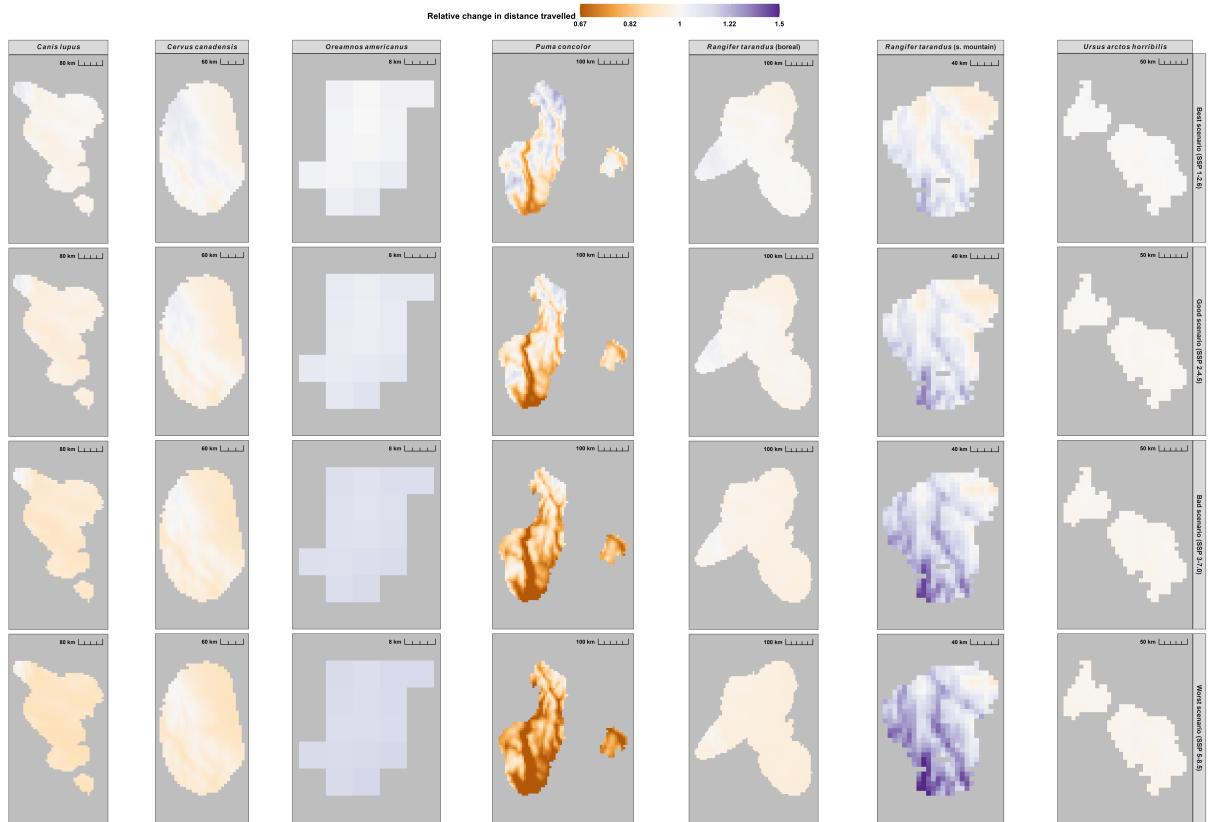


Figure 6: **Climate change will impact each species' movement rates differently.** The color scale indicates the predicted changes in distance traveled in 2100, relative to each pixel's average distance in 2025 across all four SSPs, such that 1 indicates no change, values < 1 indicate a decrease, and 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 0.50 to 1.56). The predictions only account for the predicted temperature throughout the province and ignore environmental factors such as terrain slope, soil type, and forest density.

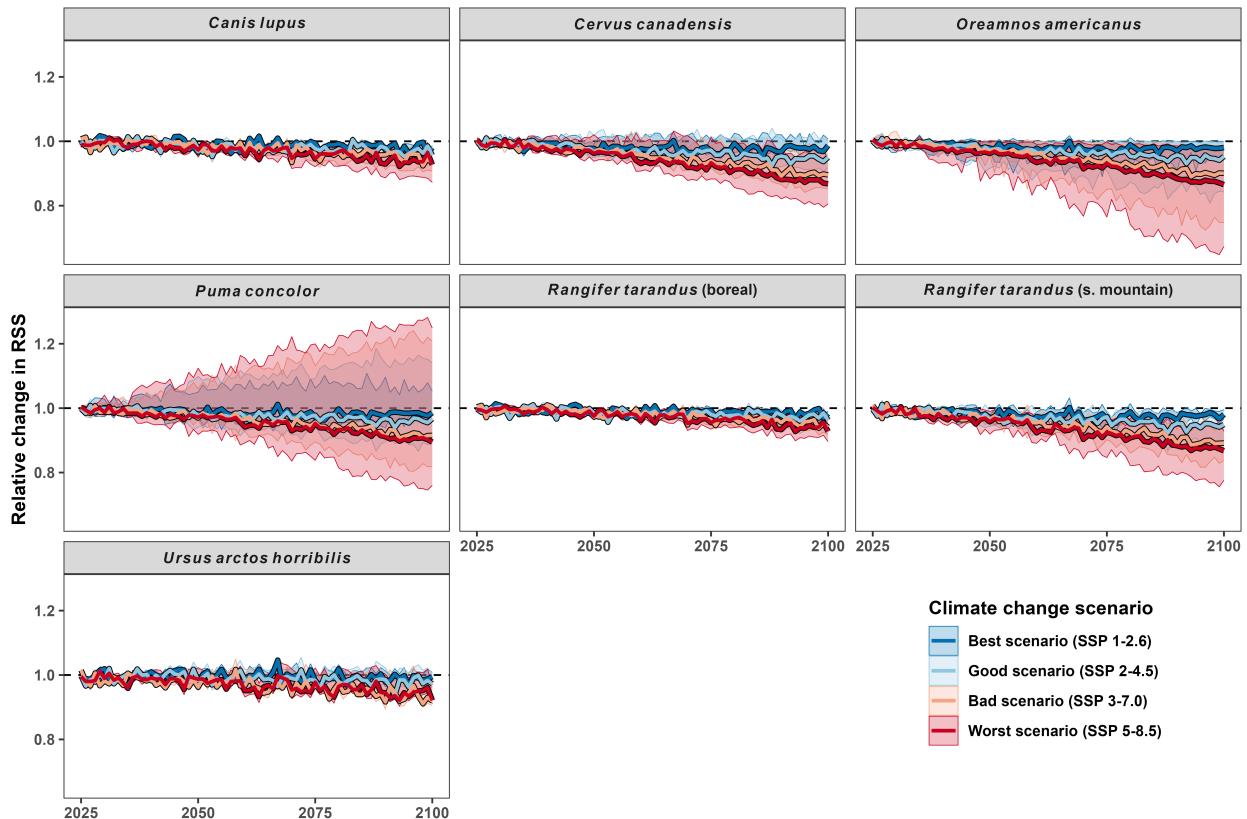


Figure 7: All species are expected to exhibit a decrease in relative selection strength (RSS) for their current range, irrespective of RSS quantile or climate change scenario, but decreases are stronger in the worse-case scenario. Lines indicate the projected change in median RSS within the species' current extent, while the ribbons indicate the range between the 95th and 5th percentiles in RSS. Changes are relative to each location's mean RSS in 2025 across the four Shared Socioeconomic Pathways (SSPs).

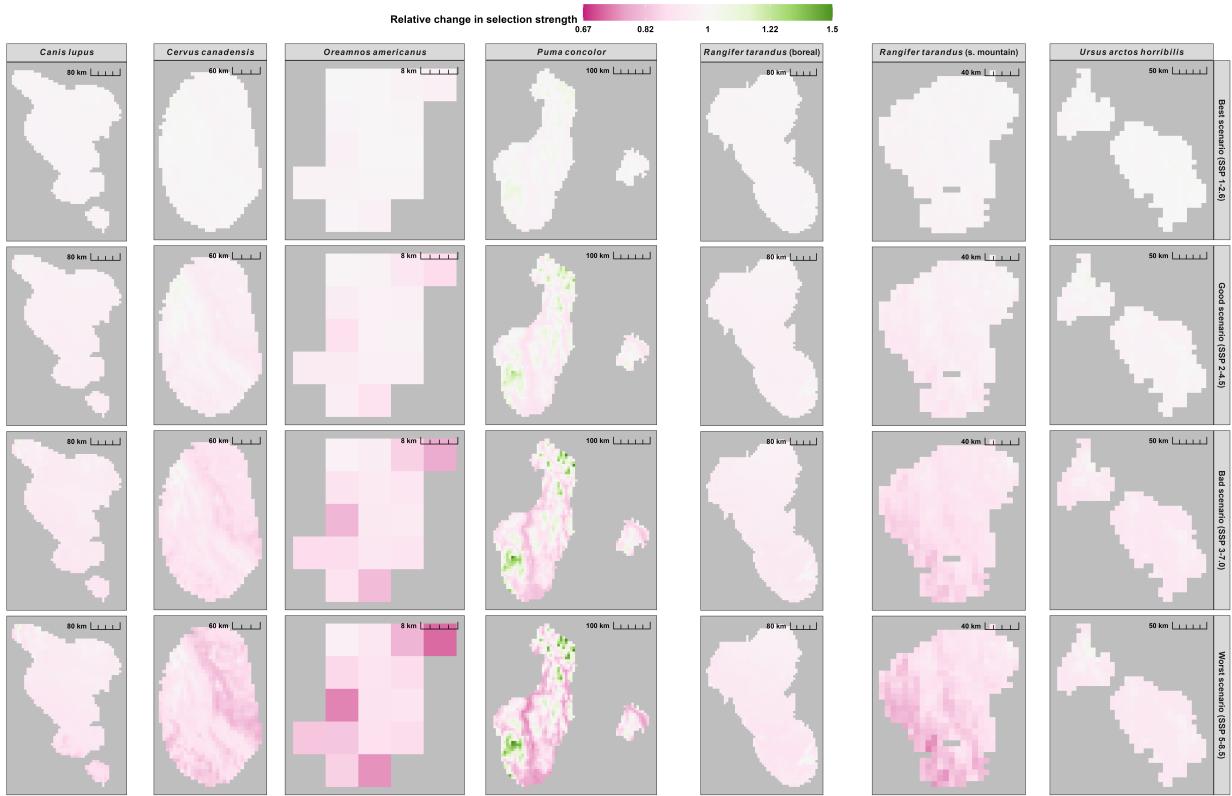


Figure 8: Climate change will impact each species' habitat relative selection strength (RSS) differently. The color scale indicates the predicted changes in RSS in 2100, relative to each location's average RSS in 2025 across all four scenarios, such that values < 1 indicate a decrease and values > 1 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 0.66 to 1.86).

331 **4 Discussion**

332 We have demonstrated that temperature is an important determinant of whether, how,
333 and where large mammals move, even while accounting for seasonality (e.g., changes in
334 photoperiod, hormones, and resources). Disentangling temperature from other drivers is
335 important for predicting how changes in climate will affect mammalian movement when
336 other drivers remain approximately constant. However, predicting mammals' responses to
337 climate change becomes increasingly complex as habitats warm and animals are exposed to
338 increasingly frequent conditions that are both extreme and novel.

339 Predicting mammals' responses at the data-scarce fringes of the surface plots in Figs. 3
340 and 4 comes with substantial uncertainty, particularly given that the responses are nonlinear.
341 At warm temperatures, mammals (and other homeotherms) overheat (Alston *et al.*, 2020;
342 Dyer *et al.*, 2023), so their movement behaviour and that of their competitors, predators,
343 and/or prey can often be substantially different from the behaviour at typical temperatures.
344 As extreme temperature events become more frequent and prolonged throughout the year
345 (Yao *et al.*, 2022; IPCC, 2023), mammals will be increasingly forced towards atypical be-
346 haviours that may alter community structures and behaviours, both during such events and
347 afterwards (Logares & Nuñez, 2012; Anderson *et al.*, 2017; Zhang *et al.*, 2023). For instance,
348 changes in climate and phenology impact the life history and behaviour of many hibernat-
349 ing mammals (Wells *et al.*, 2022), and hot weather can also affects mammals' sleep quality
350 (Mortlock *et al.*, 2024) and likelihood to enter torpor (Fjelldal *et al.*, 2021).

351 Changes in animal movement behavior may also alter the frequency and intensity of
352 human-wildlife conflict, especially with the addition of growing pressures from human de-
353 velopment and presence (Sih *et al.*, 2011; Johnson *et al.*, 2018; Weststrate *et al.*, 2024). At
354 the same time, warmer winters may reduce mammals' energetic expenditure (Berger *et al.*,
355 2018; Schmidt *et al.*, 2020), increase ease of movement as snow cover and depth decrease
356 (Leclerc *et al.*, 2021; Melin *et al.*, 2023), increase their chances of finding food or being

³⁵⁷ preyed on (Gilbert *et al.*, 2017; Hou *et al.*, 2020; Pedersen *et al.*, 2021; Slatyer *et al.*, 2022;
³⁵⁸ Sullender *et al.*, 2023), and affect the timing and duration of migrations (Sawyer *et al.*, 2009;
³⁵⁹ Leclerc *et al.*, 2021; Xu *et al.*, 2021). These changes will likely have complex consequences
³⁶⁰ for population and ecosystem structures and dynamics as prey, predators, and competitors
³⁶¹ experience altered seasonal cycles and increasingly common climate “weirding” (Bunnell *et*
³⁶² *al.*, 2011).

³⁶³ Our ability to respond changes in climate is contingent on our ability to prepare for and
³⁶⁴ predict change. However, predicting animal behaviour becomes increasingly complicated as
³⁶⁵ the conditions animals are exposed to deviate from current, typical conditions, especially
³⁶⁶ when responses are nonlinear and data are sparse. Consequently, we do not present our re-
³⁶⁷ sults as a definitive guide to how mammals in western Canada will respond to climate change.
³⁶⁸ Instead, we hope they serve as a starting point to (1) demonstrate that mammals’ movement
³⁶⁹ rates and habitat selection depend on temperature and (2) how one can estimate mammals’
³⁷⁰ changes in movement behaviour due to climate change. Additionally, communicating un-
³⁷¹ certainty in one’s estimates is crucial in assessing risk probabilistically, and appropriate
³⁷² measures of uncertainty require careful and robust modeling (Aven & Kvaløy, 2002; Ayre &
³⁷³ Landis, 2012; Czado & Brechmann, 2014).

³⁷⁴ Recent events in global politics, including global conflicts (McNutt & Hildebrand, 2022;
³⁷⁵ Tollefson, 2022) and the rapid rise in generative machine learning (more commonly: “AI,”
³⁷⁶ see Roumeliotis & Tseliakas, 2023; Van Noorden & Webb, 2023; DeepSeek-AI *et al.*, 2025) and
³⁷⁷ its prohibitive energy and water demands (Li *et al.*, 2023) and carbon footprint (Luccioni *et*
³⁷⁸ *al.*, 2024), have placed doubt on the feasibility of reaching climate change goals that seemed
³⁷⁹ achievable in the past decade (United Nations Environment Programme *et al.*, 2024). Simi-
³⁸⁰ larly, protecting a third of the world’s ecosystems (Convention on Biological Diversity, 2022)
³⁸¹ appears less achievable as global political and environmental conditions change rapidly and
³⁸² unpredictably (Sih *et al.*, 2011; Simmons *et al.*, 2021; Guenette *et al.*, 2022; Sovacool *et*
³⁸³ *al.*, 2023). Achieving the “30 by 30” goal will require international collaboration (Huang

³⁸⁴ & Zhai, 2021) as well as active partnership with local Peoples, especially Indigenous Peo-
³⁸⁵ ples (Wong *et al.*, 2020; Lamb *et al.*, 2023). Understanding the consequences of climate
³⁸⁶ change on mammals' movement behaviour is a first step towards proactively responding to
³⁸⁷ how mammals will respond to human-induced rapid environmental change (Sih *et al.*, 2011;
³⁸⁸ Williams & Blois, 2018). In the following sections, we discuss the implications of our results
³⁸⁹ in more detail. We then expand on consequences for conservation during the 21st century
³⁹⁰ and considerations for future studies.

³⁹¹ 4.1 Effects of temperature on movement rates

³⁹² The heterogeneity mammals' responses to temperature suggests that ecological communities
³⁹³ will respond to change in complex and interconnected ways. Although our models do not
³⁹⁴ account for explicit physiological or phenological changes, the surfaces in Fig. 3 suggest that
³⁹⁵ warmer temperatures cause many species to alter their daily and seasonal activity patterns
³⁹⁶ (most visible in cougars and grizzly bears). For example, when temperatures were above 0°C,
³⁹⁷ cougars moved most at night, but when temperatures were below 0°C they tended to move
³⁹⁸ more throughout the day. Throughout the year, they adapted their tolerance to temperature
³⁹⁹ and moved less when it was relatively hot (for a given time of year), especially in spring and
⁴⁰⁰ summer. The strong reduction in the mid-day movement rates of wolves, elk, cougars, and
⁴⁰¹ boreal caribou when summer temperatures were above 20°C suggests that the increasingly
⁴⁰² common and intense heat waves across British Columbia will have community-wide impacts
⁴⁰³ on movement rates, encounter rates, and potentially community structure (Martinez-Garcia
⁴⁰⁴ *et al.*, 2020). More work is necessary on quantifying interspecific responses to temperature,
⁴⁰⁵ including the effects of temperature on predation rates (but see: Cunningham *et al.*, 2021;
⁴⁰⁶ Glass *et al.*, 2021; Brivio *et al.*, 2024). The increase in intensity and frequency of extreme
⁴⁰⁷ heat events (Bunnell *et al.*, 2011; Yao *et al.*, 2022) will likely also impact the occurrence and
⁴⁰⁸ timing of hibernation (Wells *et al.*, 2022) and migration or seasonal range expansions (Morley,
⁴⁰⁹ 2021; Carbeck *et al.*, 2022; Malpeli, 2022). However, not all species may be able to adapt at

410 the current rate of climate change (Hatem *et al.*, 2014; Williams & Blois, 2018), especially
411 since landscape changes will likely depend not only on the direct effect of temperature but
412 also on cascading changes in the availability and unpredictability of resources (McLellan &
413 McLellan, 2015; Pigeon *et al.*, 2016; Mezzini *et al.*, 2025).

414 **4.2 Effects of temperature on habitat selection**

415 As with the effects of temperature on movement rates, the heterogeneity of temperature
416 effects on species' habitat selection indicates that efficient and proactive habitat conservation
417 will require taxonomic nuance. In particular, our HRSFs did not account for any explicit
418 physiological responses to temperature that may impact movement, such as changes in the
419 phenology of plants, fire, ice, or mammalian physiology (e.g., moulting, fat storages) or
420 behaviour (e.g., migration, food caching), other than as direct responses to temperature.
421 Consequently, the behavioural changes we present should be interpreted carefully. While
422 some seasonal cycles do not depend directly on temperature and may thus not be impacted
423 directly by climate change (such as those driven by photoperiod, see Liu *et al.*, 2022), the
424 predictions we present also rely on the assumption that mammals will not adapt these
425 seasonal cycles to temperature-dependent cues, such as weather (Xu & Si, 2019) or forage
426 availability (Middleton *et al.*, 2018), which may not be correct. Additionally, it is important
427 to stress the distinction between habitat selection and quality. While animals tend to select
428 for high-quality habitats (Kacelnik *et al.*, 1992; Wright, 2024), high selection strength can
429 also be a consequence of an ecological trap (Swearer *et al.*, 2021; Zuñiga-Palacios *et al.*,
430 2021).

431 **4.3 Predicted changes in movement during the 21st century**

432 Achieving the goals laid out by the “30 by 30” conservation initiative (Convention on
433 Biological Diversity, 2022) will require careful planning but often also rapid action. In the
434 case of Canada, only 13.7% of its terrestrial areas and inland waters were protected at the

435 end of 2023 (Environment and Climate Change Canada, 2024; Minister of Environment
436 and Climate Change, 2024). Additionally, efficient and effective conservation will require
437 collaboration with Indigenous and local communities to ensure Treaties are respected in the
438 process (Turner & Clifton, 2009; Wong *et al.*, 2020; Falardeau *et al.*, 2022; Lamb *et al.*,
439 2023) while also actively preparing for future change (Desjardins *et al.*, 2020; Hessami *et al.*,
440 2021).

441 The diversity in predicted changes in movement behavior by 2100 (both across species
442 and within species' current ranges) and high spatial heterogeneity in Fig. 8 highlight the
443 need for careful planning that incorporates not only reliable estimates of change but also
444 pragmatic and communicable measures of uncertainty and variability around such estimates.
445 For example, the width of the prediction intervals in Fig. 5 suggest that spatial and intra-
446 individual variation should be accounted for when deciding the location and size of protected
447 areas. Population-level means that ignore such variation can greatly limit the efficacy of
448 conservation projects (Muff *et al.*, 2020; Mortlock *et al.*, 2024). Additionally, accurate
449 estimates of the effects of changes in temperature on mammals' movement require a holistic
450 view of the direct effects of temperature on mammals' movement directly as well as its effects
451 on other drivers of movement, such as forage and prey availability (Mezzini *et al.*, 2025),
452 encounter rates (Hou *et al.*, 2020; Martinez-Garcia *et al.*, 2020), population dynamics (Smith
453 *et al.*, 2023), competitive pressure (Tórrez-Herrera *et al.*, 2020), and predation risk (Kohl *et*
454 *al.*, 2019). This complexity results in the great variation among the responses of different
455 species (and individuals), especially as populations undergo a rapid cascade of change (Botero
456 *et al.*, 2015) and animals face increasing pressures from human activity, including habitat
457 fragmentation, habitat loss, and greater human presence in wild spaces (Sawyer *et al.*, 2009;
458 Sih *et al.*, 2011; Tucker *et al.*, 2018; Rice, 2022; Rosenthal *et al.*, 2022; Weststrate *et al.*,
459 2024). As selection strength for current ranges changes (and likely decreases), some animals
460 may disperse, relocate to a new habitat, or remain within the current range despite the
461 reduced fitness and increased extinction risk (Duncan *et al.*, 2012; Logares & Nuñez, 2012;

⁴⁶² Anderson *et al.*, 2017).

⁴⁶³ **4.4 Species-specific considerations**

⁴⁶⁴ **4.4.1 *Canis lupus***

⁴⁶⁵ **4.4.2 *Cervus canadensis***

⁴⁶⁶ **4.4.3 *Oreamnos americanus***

⁴⁶⁷ **4.4.4 *Puma concolor***

⁴⁶⁸ attraction for disconnected patches of high elevation could lead to fragmentation or traps

⁴⁶⁹ **4.4.5 *Rangifer tarandus* (boreal)**

⁴⁷⁰ Increasing temperatures increased RSS for both elevations near ~500 m as well as > 1,000
⁴⁷¹ m, but such a selection is only possible if: (1) such habitats exist in the animals' range, and
⁴⁷² (2) crossing the 500 m to > 1,000 m regions is safe and attractive

⁴⁷³ **4.4.6 *Rangifer tarandus* (s. mountain)**

⁴⁷⁴ HRSFs do not account for migratory behavior due to reproduction or predation risk

⁴⁷⁵ **4.4.7 *Ursus arctos horribilis***

⁴⁷⁶ **4.5 Considerations for future studies**

⁴⁷⁷ Our work highlights three central considerations for future research: (1) telemetry sam-
⁴⁷⁸ pling rates should be designed primarily in relation to the movement timescales of the species
⁴⁷⁹ of interest (Noonan *et al.*, 2019a; Nathan *et al.*, 2022; Pease, 2024), (2) the number of indi-
⁴⁸⁰ viduals tracked and the length of each telemetry should depend not just on population size
⁴⁸¹ but also the rate of environmental change, and (3) predicting changes in movement behaviour
⁴⁸² becomes highly complex when responses are nonlinear, especially when changes depend on

483 many interacting factors (Polazzo *et al.*, 2024) and one is interested in predicting responses
484 in extreme conditions for which data are scarce (Steixner-Kumar & Gläscher, 2020).

485 While the `ctmm` movement models produced scale-independent estimates of speed (i.e.,
486 model interpretation is independent of sampling interval: Noonan *et al.*, 2019a), the accu-
487 racy, size, and stability of speed estimates still depended on the GPS sampling frequency.
488 This dependency is because coarsely-sampled movement data contains information on large-
489 scale movements (range crossings, migrations) but not fine-scale movements, including first-
490 order habitat selection (Johnson, 1980). Using the boreal caribou as an example, the 13-hour
491 sampling interval allows us to reasonably estimate the caribou's movement path at a tempo-
492 ral scale of approximately 13 hours (or greater), but we cannot produce reasonable movement
493 trajectories at a much finer (e.g., hourly) scale. Nathan *et al.* (2022) provides additional
494 examples of how the frequency of location data affects the results that can be inferred by
495 modeling movemet behavior. Consequently, we suggest being cautious when comparing esti-
496 mated movement behaviours across species, even though all predictions have been corrected
497 to the hourly timescale by predicting for 1-hour time intervals (i.e., `dt_hours = 1`). Ide-
498 ally, sampling schedules should be fine enough to reconstruct animals' movement movement
499 paths. Good estimates of an animal's speed and trajectory require telemetry locations to
500 be taken more often than the animal's directional persistence (Noonan *et al.*, 2019a), so
501 that, on average, the dataset contains multiple locations in between changes in direction.
502 What constitutes a change in direction depends on what movement scale one is investigating.
503 Small-scale movements and first-order spatial selection will require more frequent sampling
504 than migratory movement or second-order and third-order spatial selection. While `ctmm`
505 movement models are scale-invariant in that any model can be scaled to larger or smaller
506 areas and timescales, the model estimates are not independent of the scale of the sampling
507 frequency.

508 When landscapes are relatively predictable across years, a larger number of sampled
509 individuals is likely preferable over the duration of each tracking period. The greater number

510 of tracked animals allows one to quantify the variance across individuals, including the
511 range of conditions and environments that individual animals are in. A good estimate of
512 inter-individual variance provides better coefficient estimates along with more appropriate
513 measures of uncertainty. However, when conditions across years are stochastic, multi-year
514 telemetries allow one to better estimate inter-annual variation without conflating it with
515 inter-individual differences. Given the widespread, rapid, and accelerating changes across
516 many habitats (particularly at high elevations and at high latitudes), we suggest researchers
517 focus on long-term telemetry datasets to quantify the effects of intra-annual variability while
518 increasing the ranges of temperatures each individual is observed in. Longer observational
519 periods can also improve the chances of observing different community dynamics, such as
520 shifts in predator-prey dynamics.

521 Temperature affects many aspects of mammalian physiology and behavior, including en-
522 ergetics, sleep, and movement behavior. Climatic changes during the last two centuries have
523 exposed many mammals to novel and increasingly extreme environmental conditions that
524 have led to visible changes that impact not only individuals but also ecological and human
525 communities. However, quantifying the effects of climate change is often complex, espe-
526 cially as conditions become increasingly different and extreme events become increasingly
527 common. Accurately quantifying the nonlinear effects of temperature on when, how, and
528 where mammals move requires careful data collection and model design. We have presented
529 a multi-species analysis of the effects of temperature on mammalian movement rates and
530 habitat selection in hopes that other researchers can leverage this framework and models
531 to expand our understanding of how temperature affects the movement behavior of other
532 species, including smaller mammals, more elusive species, and non-mammal animals. Un-
533 derstanding of how temperature affects each species in a community will allow us to begin
534 making community-level inferences of how temperature will affect intra-specific interactions
535 from a movement behavior perspective (Nathan *et al.*, 2008, 2022; Martinez-Garcia *et al.*,
536 2020). While adopting such a perspective is surely not simple, it would result in more com-

537 plete estimates of the effects of climate change on community ecology, particularly when
538 species are exposed to rapid change in many important variables. Future work should ex-
539 plore the effects of temperature on movement behavior while accounting for finer-scale and
540 species specific variables that were not accounted for in this study. Examples of these include
541 temporally dynamic measures of forest type and age, canopy density, competitive pressures,
542 forage availability, and predator avoidance, or environmental stochasticity. However, many
543 of these data not available, so we also suggest that more work be done on quantifying such
544 measures using spatiotemporally dynamic models and sufficiently fine resolutions.

545 **5 Author contributions**

546 SM performed the data cleaning, ran the analyses, and wrote the majority of the
547 manuscript. CHF wrote code for estimating instantaneous movement speeds. MJN
548 conceived of the project idea and supervised SM throughout the project. All other authors
549 contributed telemetry data and contributed to the interpretation of the results for their
550 species of interest. All authors contributed to reviewing the manuscript.

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