

The heat is on: Rising temperatures alter how and where mammals
move

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Abstract

Widespread warming during the last century has caused many terrestrial mammals to change how and where they move, with cascading effects on fitness, habitat selection, and community structure. Previous studies have estimated the effects of temperature on mammalian movement behaviour, but many did not disentangle them from seasonal behavior cycles. 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 movement rates and habitat selection of six large-bodied mammalian species throughout western Canada between 1998 and 2023. We show that temperature is a strong determinant of how and where mammals move, and we predict that climate change will have significant impacts on mammals' movement rates and habitat selection throughout the 21st century. We found that species did not respond uniformly to rising temperatures, so community-level responses will likely be complex as some species move more and others less. Median habitat selection strength decreased for all species, but some species showed increased selection strength for higher altitudes. Consequently, our results suggest that all six species may shift their range in the coming decades as their selection strength for their current ranges weakens. As climate change exposes mammals to novel environmental conditions, predicting changes in animal behavior and community structure will become crucial for effectively and proactively understanding mammalian movement behavior and protecting high-quality habitat. We thus present our work using a flexible approach that can be adapted for different species and spatiotemporal scales, and we conclude by providing suggestions for future research, with particular attention to the study design, statistical modeling, and forecasting.

¹ **1 other refs**

- ² • Gerlich *et al.* (2025): effects of temperature on fly movement in the arctic
- ³ • “Potential changes in climate indices in Alberta under projected global warming of
- ⁴ 1.5–5 °C” (<https://www.sciencedirect.com/science/article/pii/S2214581823000770#fig0015>)
- ⁵ • Global vulnerability of marine mammals to global warming: <https://doi.org/10.1038/s41598-019-57280-3>
- ⁶ • marine turtles shift and lose habitat with temperature: <https://www.science.org/doi/10.1126/sciadv.adw4495>
- ⁷ • changes in temperature change phenology and movement behavior as a consequence Ger-
- ⁸ lich *et al.* (2025)
- ⁹ • Walker *et al.* (2019): Global climate change and invariable photoperiods: {A} mismatch that jeopardizes animal fitness
- ¹⁰
- ¹¹
- ¹²
- ¹³

¹⁴ **2 Introduction**

¹⁵ For most animals, movement is a rapid and low-cost response to a variety of stimuli (Nathan
¹⁶ *et al.*, 2008). Animals move to optimize resource use (e.g., food, water, shelter; Charnov,
¹⁷ 1976; Kacelnik *et al.*, 1992; Mezzini *et al.*, 2025), optimize habitat use (Schwerdt *et al.*,
¹⁸ 2024; Winter *et al.*, 2024), and avoid predators and competitors (Tórrez-Herrera *et al.*,
¹⁹ 2020; Peterson *et al.*, 2021; Bartashevich *et al.*, 2024; Tan *et al.*, 2024). However, ambient
²⁰ temperature affects mammals' movement rates by altering the energetic cost of movement
²¹ (McNab, 1970; Taylor *et al.*, 1982; Brown *et al.*, 2004; Fuller *et al.*, 2016; Jahn & Seebacher,
²² 2022) and the risk of hyperthermia (Hetem *et al.*, 2014; Dyer *et al.*, 2023). Animals may
²³ search for a short-term buffer from extreme heat or cold via thermal refugia (Hannah *et al.*,
²⁴ 2014; Elmore *et al.*, 2017; Attias *et al.*, 2018; Arechavala-Lopez *et al.*, 2019; Gulland *et al.*,
²⁵ 2022), which may even be preferred over forage abundance (Hall *et al.*, 2016). By altering
²⁶ mammals' movement speed and habitat use (jointly, their movement behavior: Nathan *et al.*,
²⁷ 2008, 2022), ambient temperature also affects the consequences of movement behavior, such
²⁸ as encounter rates with resources (Mezzini *et al.*, 2025), humans (Weststrate *et al.*, 2024),
²⁹ predators, prey, or competitors (Martinez-Garcia *et al.*, 2020; Glass *et al.*, 2021; Brivio *et*
³⁰ *al.*, 2024). Behavioral changes to temperature are exacerbated in extreme cold (Wilson *et*
³¹ *al.*, 2001; Berger *et al.*, 2018) and extreme heat (Powers *et al.*, 2017; Alston *et al.*, 2020;
³² Giroux *et al.*, 2023; Verzuh *et al.*, 2023).

³³ Mammals are particularly susceptible to adverse effects from excessive heat (Sherwood
³⁴ & Huber, 2010). While extreme cold often leads to reduced movement, provided that in-
³⁵ dividuals can find refuge and take advantage of their body heat (Berger *et al.*, 2018; Hou
³⁶ *et al.*, 2020; Glass *et al.*, 2021), extreme heat can often result in more rapid and serious
³⁷ physiological damage (Jessen, 2001; Sherwood & Huber, 2010; Mota-Rojas *et al.*, 2021).
³⁸ Due to mammals' difficulty at dissipating heat, particularly when ambient temperatures are
³⁹ near or above their body temperature, they are particularly sensitive to extreme heat, par-

40 ticularly if they have a large body size (Dyer *et al.*, 2023; Verzuh *et al.*, 2023). Furthermore,
41 species that experience narrow temperature ranges (i.e., ‘temperature specialists’) tend to
42 be more sensitive to changes (e.g., giant anteaters, *Myrmecophaga tridactyla*: Giroux *et al.*,
43 2023), while species that experience wide ranges of temperature variation (i.e., ‘temperature
44 generalists’) can adapt more easily to change (Levins, 1974; Botero *et al.*, 2015; Dupont *et*
45 *al.*, 2024). Still, generalists’ greater adaptability is tested when they are subject to changes
46 that are more severe (McCain, 2019), affect many factors (e.g., temperature, snow depth,
47 ecosystem phenology, and resource availability: Polazzo *et al.*, 2024), or are too rapid to
48 respond within the span of a lifetime or a few generations (Levins, 1974; Fuller *et al.*, 2016;
49 Xu *et al.*, 2021).

50 ... Temperature also has indirect effects on movement through other drivers of movement
51 behaviour, such as trophic interactions (Hegel *et al.*, 2010), snow depth and density (Mont-
52 gomery *et al.*, 2019; Leclerc *et al.*, 2021; Melin *et al.*, 2023), altered phenology [Bunnell *et*
53 *al.* (2011);], and the frequency and intensity of extreme events (Bunnell *et al.*, 2011; Zhang
54 *et al.*, 2023), including forest fires, droughts, and extreme weather (Bunnell *et al.*, 2011;
55 Duncan *et al.*, 2012; Merkle *et al.*, 2016; Berger *et al.*, 2018; Slatyer *et al.*, 2022; Zurowski,
56 2023). Changes in temperature thus affect how animals move (e.g., movement frequency and
57 speed – their movement behaviour: Nathan *et al.*, 2008; Dyer *et al.*, 2023) and where they
58 move to (i.e., their habitat selection: Merkle *et al.*, 2016; Alston *et al.*, 2020; Giroux *et al.*,
59 2023).

60 In the last 200 years, many ecosystems experienced widespread warming that resulted
61 in milder and shorter winters, hotter and longer summers, and a greater risk of extremely
62 high temperatures (IPCC, 2023). Over the next 100 years, these changes are expected to
63 worsen and continue to impact mammals’ fitness, movement behaviour, and habitat selec-
64 tion as animals cope with growing heat stress (Deb *et al.*, 2020; Woo-Durand *et al.*, 2020)
65 and more frequent and intense extreme events (Bunnell *et al.*, 2011), along with increas-
66 ing anthropogenic pressure (Sawyer *et al.*, 2009; Sih *et al.*, 2011; Weststrate *et al.*, 2024).

67 Consequently, it remains unclear how or whether species will be able to respond to climate
68 change in the current century (Deb *et al.*, 2020; Woo-Durand *et al.*, 2020; Verzuh *et al.*,
69 2023), especially when populations fail to adapt to changes (Botero *et al.*, 2015; Sawyer *et*
70 *al.*, 2019) or are physiologically incapable to do so (Sherwood & Huber, 2010; Williams &
71 Blois, 2018). Uncertainty in future conditions and their consequences on ecosystems present
72 a need for a comprehensive understanding of (1) the direct effects of temperature on animal
73 movement behaviour and (2) the implications such changes and uncertainty will have on
74 populations and species' adaptability and resiliency, as well as overall community structure.
75 Recent work has documented the effects of climate change on mammals' ranges (Leclerc *et*
76 *al.*, 2021), movement behaviour (Melin *et al.*, 2023), thermoregulation (Mota-Rojas *et al.*,
77 2021), and trait-based responses (e.g., body size, activity time, and elevational and lati-
78 tudinal distribution McCain, 2019). However, it is still unclear how mammals will adapt
79 their small-scale movement and habitat selection to changes in temperature during the 21st
80 century (IPCC, 2023; but see Hetem *et al.*, 2014; Winter *et al.*, 2024).

81 Understanding the direct and indirect impacts of temperature on mammalian movement
82 is essential for decision makers to respond to change in a proactive manner (Sawyer *et al.*,
83 2009; McCain, 2019). Western Canada is currently experiencing rapid widespread warming
84 (Turner & Clifton, 2009; Kienzle, 2018; Dierauer *et al.*, 2021), phenological shifts (Kienzle,
85 2018; Basu *et al.*, 2024; Tysor, 2025), and more frequent and intense extreme events (Zhang
86 *et al.*, 2023), including forest fires (Zurowski, 2023). As we approach the deadline for the
87 "30 by 30" conservation initiative, a global effort to conserve 30% of the world's lands and
88 oceans by 2030 (Convention on Biological Diversity, 2022), decision makers must understand
89 which areas will be of greatest value for maximizing the project's effectiveness. Predicting
90 how climate change will affect how, when, and where animals will move is necessary for
91 identifying landscape dynamics and value will evolve throughout the century. Failing to
92 understand how changes in temperature will affect mammalian movement behaviour and
93 habitat selection will hinder our ability to respond to the current climate crisis and make

94 decisions that are viable in the long term.

95 This paper provides a framework for quantifying the effects of proximal air temperature
96 on animal movement using quantitative methods that are flexible and statistically robust.
97 We present results for six large-bodied terrestrial mammal species in western Canada (wolves:
98 *Canis lupus*, elk: *Cervus canadensis*, mountain goats: *Oreamnos americanus*, cougars: *Puma*
99 *concolor*, boreal and southern mountain caribou: *Rangifer tarandus*, and grizzly bears: *Ursus*
100 *arctos horribilis*; Table 1). Using over 25 years of telemetry data throughout a large
101 spatial range of western Canada and hourly air temperature data, we estimate how these
102 mammals altered their probability of movement, speed when moving, and habitat selec-
103 tion in response to temperature. We then pair the estimated responses with climate change
104 projections to forecast the species’ movement during the 21st century under different climate-
105 change scenarios (referred to as Shared Socioeconomic Pathways, SSP, Riahi *et al.*, 2017).
106 We disentangle the direct and indirect effects of temperature on the movement behaviour
107 of terrestrial mammals and discuss the consequences of these changes at the individual,
108 population, and community levels.

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 |

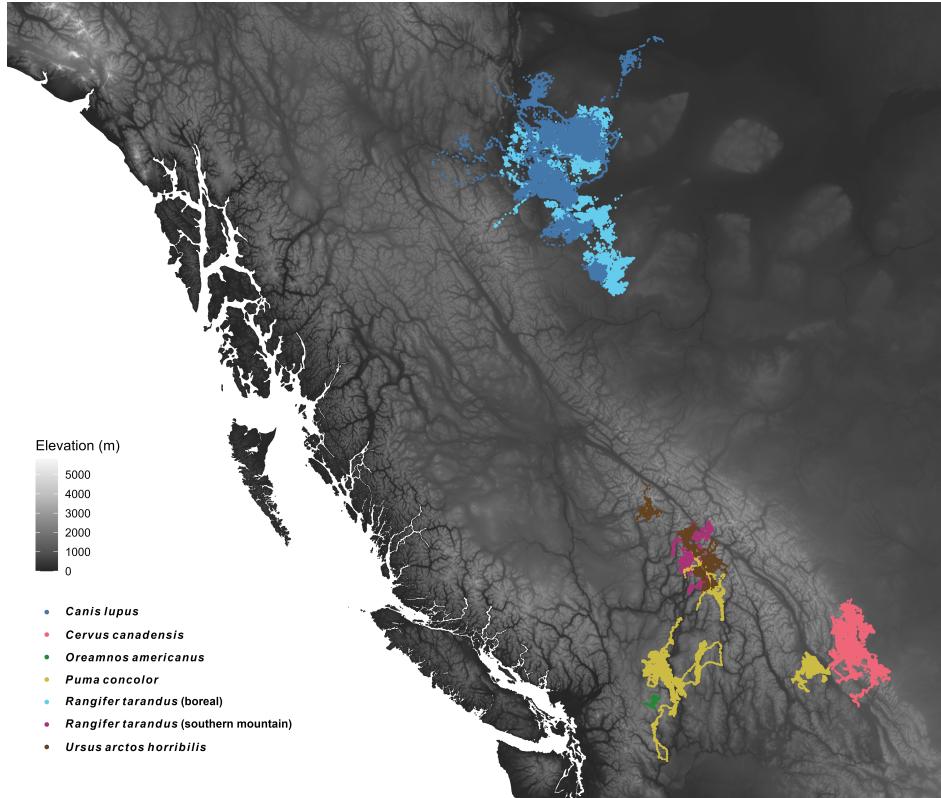


Figure 1: GPS telemetry data for the six species in this study (dots) over a digital elevation model for the study area.

109 3 Methods

110 3.1 Datasets used

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

119 **3.1.1 GPS telemetry data**

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

131 **3.1.2 Historical temperature data and temperature projections**

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

138 We obtained rasters of projected monthly average temperature for the study region at a
139 0.08° spatial resolution from 2020 to 2100 under the different SSPs via the `climatenetR` pack-
140 age (version 1.0, Burnett, 2023) for R. Since the climate projections only provided monthly
141 means and ranges but no measures of variance or distributional assumptions, we used the
142 hourly ERA5 reanalyzed data for western Canada from 1998 to 2023 (extremes included,
143 Hersbach *et al.*, 2023) to calculate within-month variance in temperature, which we defined as
144 the variance within a given pixel, month, and year. We then modeled the estimated variance

145 using a GAM for location and scale (GAMLS, Rigby & Stasinopoulos, 2005; Stasinopoulos &
146 Rigby, 2007; section 7.9 in Wood, 2017). The linear predictor for the location (i.e., the mean)
147 included smooth terms of the within-pixel monthly mean temperature (within each year),
148 month (as a cyclic smooth), a two-dimensional smooth of space, and a tensor interaction
149 product term of space and month. The linear predictor for the scale term (which governs the
150 mean-variance relationship) included smooth terms of the monthly mean, month, and space.
151 We did not include a smooth of year to avoid unrealistic projections when extrapolating
152 beyond the range of historical data.

153 We simulated hourly variation in future weather by assuming hourly temperature fol-
154 lowed a normal distribution with mean specified by the monthly `climatenar` climate pro-
155 jections and variance as specified by the Gamma GAMLS. For each month within each year
156 from 2020 to 2100, we simulated hourly weather by including temperatures from the 0.1 to
157 the 0.9 quantile by increments of 0.1, and we weighted each quantile proportionally to the
158 (normalized) Gaussian probability density for each quantile.

159 3.1.3 Resource rasters

160 We estimated percent forest cover and distance from water using the rasters created by
161 Tuanmu & Jetz (2014). We calculated total forest cover by summing the temporally
162 static rasters of evergreen/deciduous needle-leaf trees, evergreen broadleaf trees, deciduous
163 broadleaf trees, and mixed/other trees (raster classes 1-4, respectively). We converted the
164 raster of percent cover of open water (class 12) to a binary raster of pixels with water (cover
165 > 0%) or without water (cover = 0%) and then calculated each pixel's distance from the
166 nearest pixel with water using the `distance()` function from the `terra` package. Finally,
167 we obtained two digital elevation models using the `get_elev_raster()` function from the
168 `elevatr` package (version 0.99.0, Hollister *et al.*, 2023): We used a raster with a zoom
169 of 6 (0.009°) for model fitting and one with a zoom of 3 (0.08°) for downloading climate
170 change projections via `climatenar`. All final rasters and code are available on GitHub at

171 <https://github.com/QuantitativeEcologyLab/bc-mammals-temperature>.

172 **3.2 Estimating mammals' instantaneous speeds**

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

180 Since 'ctmm's movement models assume stochastic but non-zero speeds (i.e., a sin-
181 gle, stochastic moving state), data-informed speeds needed to be corrected so that the
182 minimum instantaneous speed could be 0. We performed this correction by subtracting
183 each model's mean speed while assuming speeds were χ^2 -distributed. The function we
184 used is available on GitHub at <https://github.com/QuantitativeEcologyLab/bc-mammals->
185 [temperature/blob/main/functions/detrend_speeds.R](https://github.com/QuantitativeEcologyLab/bc-mammals-temperature/blob/main/functions/detrend_speeds.R). To avoid artifacts due to excessively
186 small, non-zero speeds, we determined whether an animal was moving or not using a k -means
187 algorithm with 2 clusters for each species' detrended speeds. When the algorithm clearly
188 failed to discriminate between states, we estimated the split point using the inflection points
189 in histograms of the detrended speeds (Fig. B1).

190 **3.3 Estimating the effects of temperature on mammals' movement**

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

196 **3.3.1 Disentangling direct and indirect effects**

197 In this study, we separate the effects of temperature on mammalian movement into direct
198 and indirect effects. We call “direct” all effects that impact movement behavior causally
199 without first impacting another variable (Fig. 2). For example, in Fig. 2A, whether a
200 grizzly bear is moving in a given moment directly depends on time of day and day of year,
201 since it will not be moving when sleeping or hibernating. However, time of day and day of
202 year also impact its movement behavior indirectly because its sensitivity to temperature will
203 also depend on time of day and day of year. Thus, both time of day and day of year also
204 impact movement frequency indirectly by altering the effect of temperature on movement
205 frequency. Failing to disentangle the effects of these three variables will lead to incorrect and
206 likely confusing estimates for the causal effect of temperature on movement behavior, since
207 causal and non-causal relationships would be indistinguishable (McElreath, 2020).

208 Indirect effects of temperature also include all effects that can be controlled by altering
209 an animal’s habitat (its geographic space *sensu* Matthiopoulos, 2022). For example, in Fig.
210 2B, an increase in temperature may push an animal to prefer higher forest cover in search of
211 shade, and conservationists can mitigate these indirect effects of temperature by increasing
212 the availability of forested areas, since the effect of temperature on movement is conditional
213 on forest cover availability. In contrast, the animal may avoid moving if temperatures are
214 above 35°C, irrespective of its geographic and environmental space (*sensu* Matthiopoulos,
215 2022). In this case, it is not possible to mitigate the effects of temperature on movement
216 behaviour (other than changing temperature directly).

217 **3.3.2 Effects of temperature on movement rates**

218 We estimated the effects of temperature (°C) on mammals’ instantaneous movement state
219 (moving or not) and speed when moving using two Hierarchical Generalized Additive Models
220 (HGAMs, see Pedersen *et al.*, 2019 and the code chunk below) with the `mgcv` package for R
221 (version 1.9-1, Wood, 2017). The first HGAM estimated the probability that an animal was

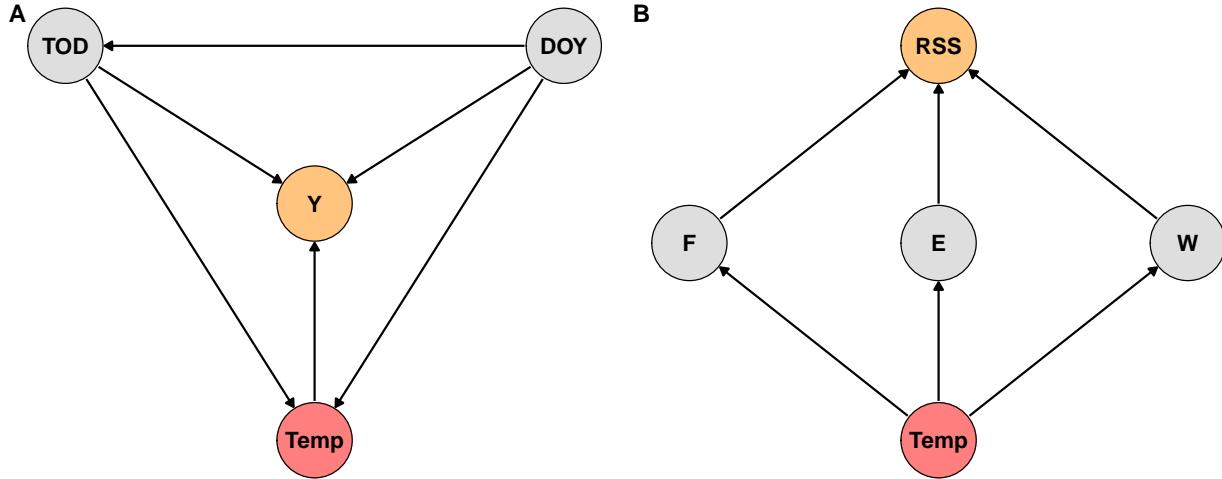


Figure 2: Directed Acyclical Graphs (DAGs) assumed for inferring the causal effects of temperature (Temp) on movement behavior. (A) DAG for the probability of moving, speed when moving, or distance traveled (Y) while accounting for the effects of time of day (TOD), day of year (DOY), and their interaction 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.

222 moving, $P(M)$, with a binomial family of distributions and logit link function. The response
 223 variable `moving` was coded as 1 if moving and 0 if not. The second HGAM estimated an
 224 animal's speed when moving (`speed`) with a gamma family of distributions and log link
 225 function.

226 The HGAMs included random intercepts for each animal (`s(animal, bs = 're')`),
 227 fixed-effect intercepts for each species (`species`), and species-level by smooths (`s(...,`
 228 `by = species)`), which allowed each species' term to be estimated independent of other
 229 species (see model I in Figure 4 of Pedersen *et al.*, 2019). The `by` smooths accounted for
 230 trends in time of day (in Pacific Daylight Time; `tod_pdt`), day of year (`doy`), and tempera-
 231 ture (`temp_c`). The models also had three tensor product interaction terms (`ti()`) by each
 232 species: (1) day of year and time of day, (2) temperature and time of day, and (3) tempera-
 233 ture and day of year. These three terms accounted for: (1) seasonal changes in day length,
 234 (2) hourly changes in the response to temperature (e.g., changes in nocturnality), and (3)
 235 seasonal changes in the response to temperature (e.g., changes in coats and migration tim-
 236 ing). Finally, smooth terms of log-transformed hours between GPS locations (`dt`) accounted
 237 for irregular sampling rates. A global term of `log(dt)` accounted for the overall effect

238 of sampling interval, while a factor-smooth interaction term (`s(log(dt), species, bs =`
239 `'fs')`) allowed for species-level deviations from the global term while assuming a common
240 smoothness parameter across species (see model GS in Figure 4 of Pedersen *et al.*, 2019).

241 The HGAMs accounted for the cyclicity of time of day and day of year using cyclic
242 cubic splines (`bs = 'cc'`, see p. 202 of Wood, 2017). We fit the models with fast Restricted
243 Maximum Likelihood ('`fREML`') and discretized covariates (`discrete = TRUE`) to optimize
244 computational efficiency with no appreciable losses to model performance (Appendix B;
245 Wood *et al.*, 2015, 2017; Li & Wood, 2020). Together, the binomial HGAM and the gamma
246 HGAM inform us on an animal's long-term average speed, since it is the product of the
247 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)))

```

248 3.3.3 Effects of temperature on habitat selection

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

260 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)
```

261 Smooth effects of percent forest cover, elevation, and distance to water accounted for
262 the species-level average selection strength for each resource. A random effect for each in-
263 dividual animal (`s(animal, bs = 're')`) corrected for uneven sampling across individuals,
264 while factor smooth interaction terms (`bs = 'fs'`) accounted for individual-level resource
265 selection (i.e., individual-level deviations from the species-level average; Jeltsch *et al.*, 2025).
266 Tensor interaction product terms (`ti()`) of the three resources and temperature estimated
267 the change in resource selection at different temperatures. Finally, we included marginal
268 smooth terms of temperature to account for species- and individual-level sampling biases
269 over temperature (e.g., sampling more during warm periods). Detections were weighted
270 proportionally to their degree of independence from other temporally proximate detections
271 (`weights = weight` – Appendix B; Alston *et al.*, 2022), while quadrature points had a weight
272 of 1. Quadrature points were obtained using all raster cells in the 99.9% AKDE percentile.
273 The number of quadrature locations greatly outnumbered the number of observed locations
274 (Fig. B12), especially after accounting for weighting based on the degree of autocorrelation
275 and the number of home range crossings (Fig. B13).

276 **4 Results**

277 Overall, 2.6% of GPS locations had temperatures lower than -20°C , while 6.5% had temper-
278 atures above 20°C , and temperature ranges differed across species (Table 2, Fig. B2). At 0°C ,
279 species differed in overall mean probabilities of movement (range: 0.05 – 0.31), mean speed
280 when moving (range: 0.42 – 2.67 km/h), and mean distance traveled (i.e., $P(M) \times \mathbb{E}(S)$,
281 range: 0.04 – 0.61 km/h; Table 3). Grizzly bears tended to move least often ($P(M) \approx 0.05$),
282 while wolves and cougars moved most often ($P(M) \geq 0.22$). When moving, mountain goats
283 and southern mountain caribou moved the slowest ($\mathbb{E}(S|M) \approx 0.43$ km/h), while wolves
284 had the highest mean speed when moving ($\mathbb{E}(S|M) \approx 2.64$ km/h). Consequently, wolves
285 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 |

286 Near 0°C , wolves selected for dense forest cover ($\gtrapprox 50\%$), elevations near 1 km, and
 287 distances from water < 10 km; elk selected for forest cover near 50%, elevations between
 288 1 and 2 km, and distances from water of 5-15 km; mountain goats selected for sparse (<
 289 50%) forest cover, elevations between 1 and 2 km; cougars selected for dense forest cover,
 290 an elevation of ~ 1 km, and distances from water < 10 km; boreal caribou selected for
 291 intermediate to dense forest cover, elevations near 500 m, and distances from water < 10
 292 km; southern mountain caribou selected for dense forest cover, elevations near 2 km, and
 293 distances from water < 5 km; and grizzly bears selected for sparse forest cover (25-50%),
 294 elevation near 1 km, and distances from water < 2 km.

295 There was relatively strong agreement between models with and without temperature
 296 (Figs. B3, and B14), but including temperature always resulted in better fits. All analyses
 297 of deviance showed that temperature significantly affected movement behavior (all p-values
 298 $< 2.2 \times 10^{-16}$; all $\Delta\text{AIC} \geq 342$; Table B2 and following pages in Appendix B). Accounting
 299 for temperature resulted in a simpler HRSF for mountain goats (lower model degrees of
 300 freedom) that fit the data better (lower deviance), and hence no test was necessary to show
 301 that the inclusion of temperature produced a better fit.

302 **4.1 Effects of temperature on movement rates**

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

320 **4.2 Effects of temperature on habitat selection**

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

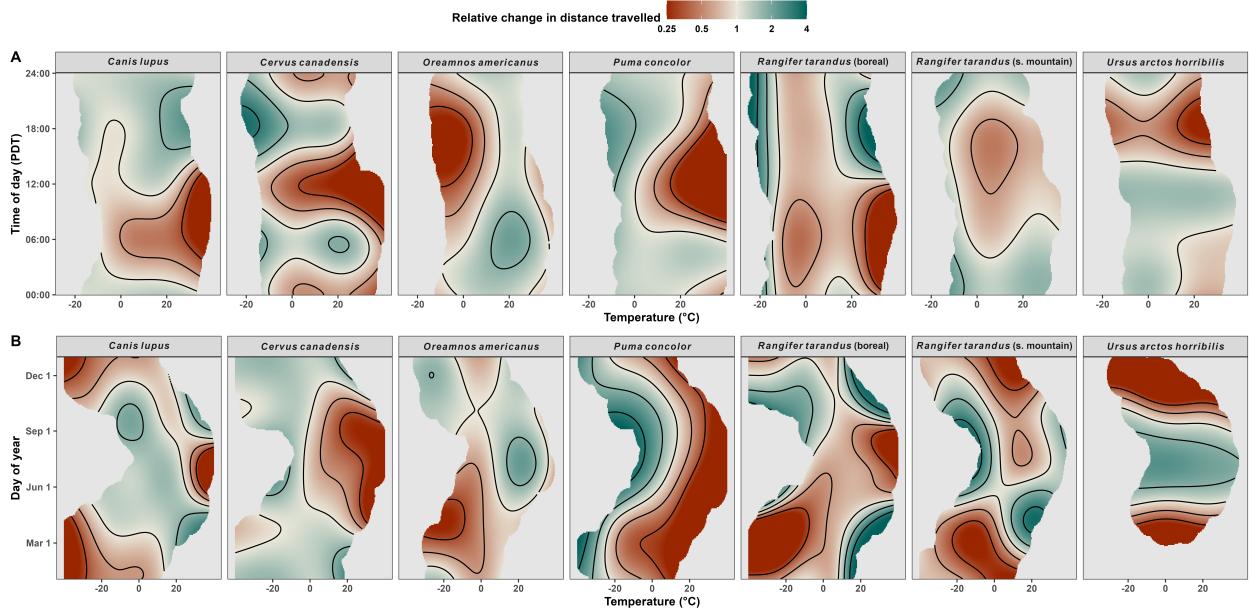


Figure 3: Temperature is a strong determinant of how far and when mammals travel. The fill indicates the estimated effects of temperature on the relative change in distance travelled (probability of moving times mean speed when moving) over time of day on June 1st (**A**) and day of year at 12:00 PDT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

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

336 4.3 Predicted changes in movement during the 21st century

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

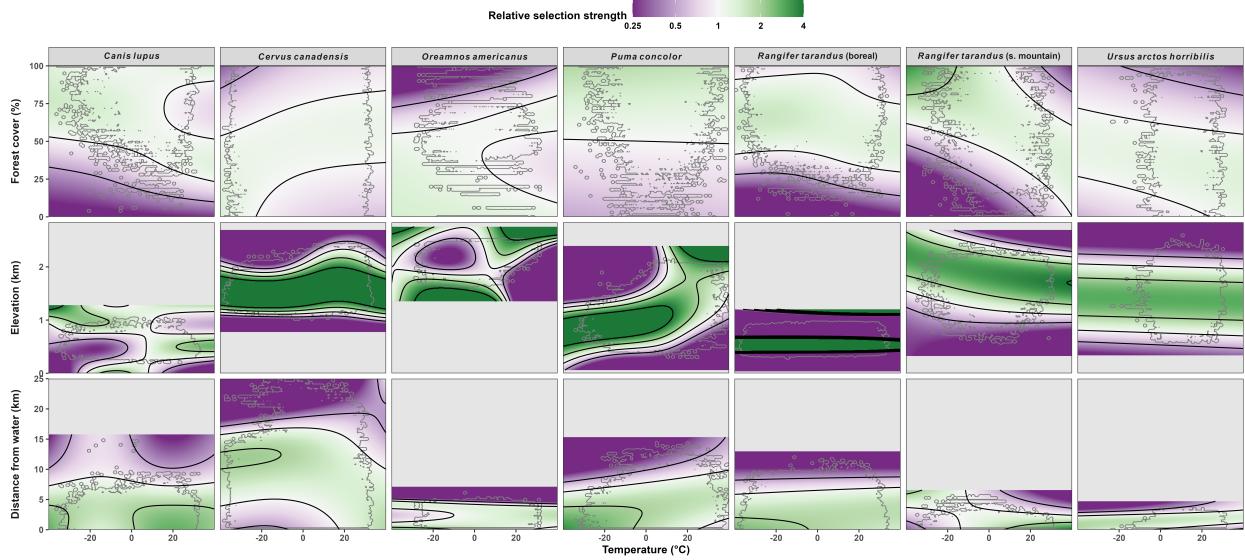


Figure 4: **Temeperature strongly affects mammals' habitat selection.** Estimated relative selection strength (RSS) for forest cover (%), elevation (km), and distance from water (km) as a function of temperature. The grey contours indicate the extent of each species' observed data. RSS values were re-centered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

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

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

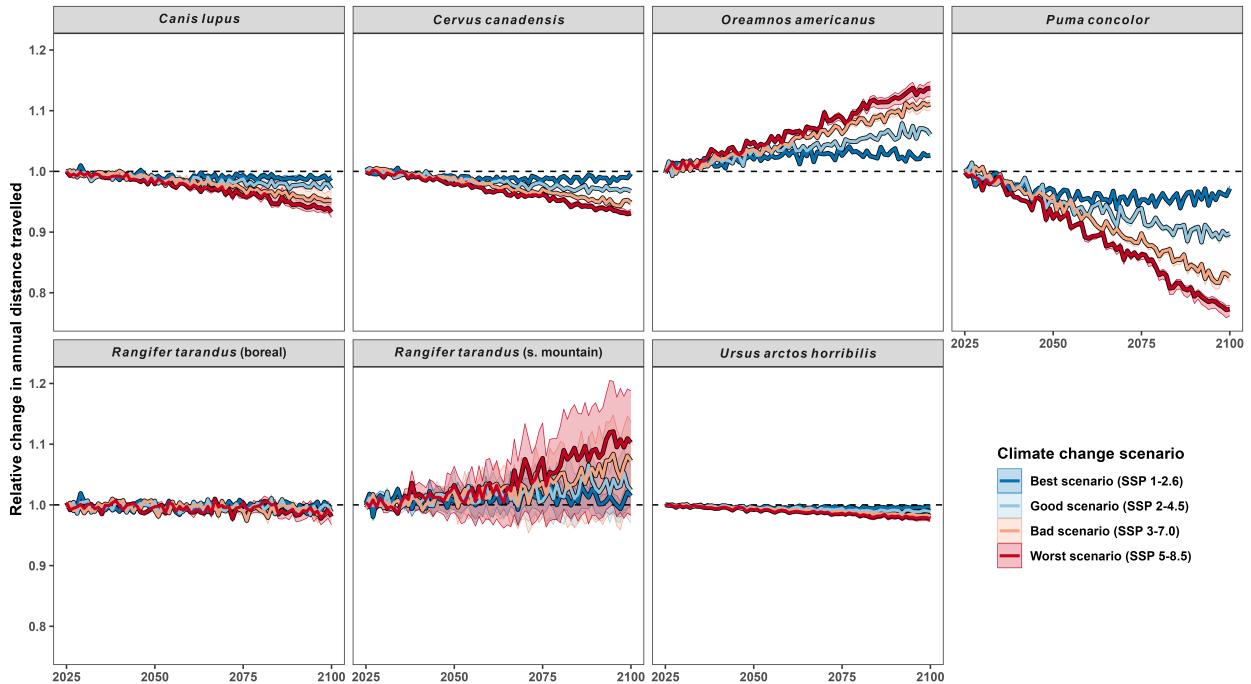


Figure 5: **The direction and magnitude of changes in movement rates due to climate change varies among species, but worse climate-change scenarios result in the greatest change.** Lines indicate the median projected change in distance travelled (probability of moving times speed when moving) due to changes in temperature within each species' observed extent. 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.

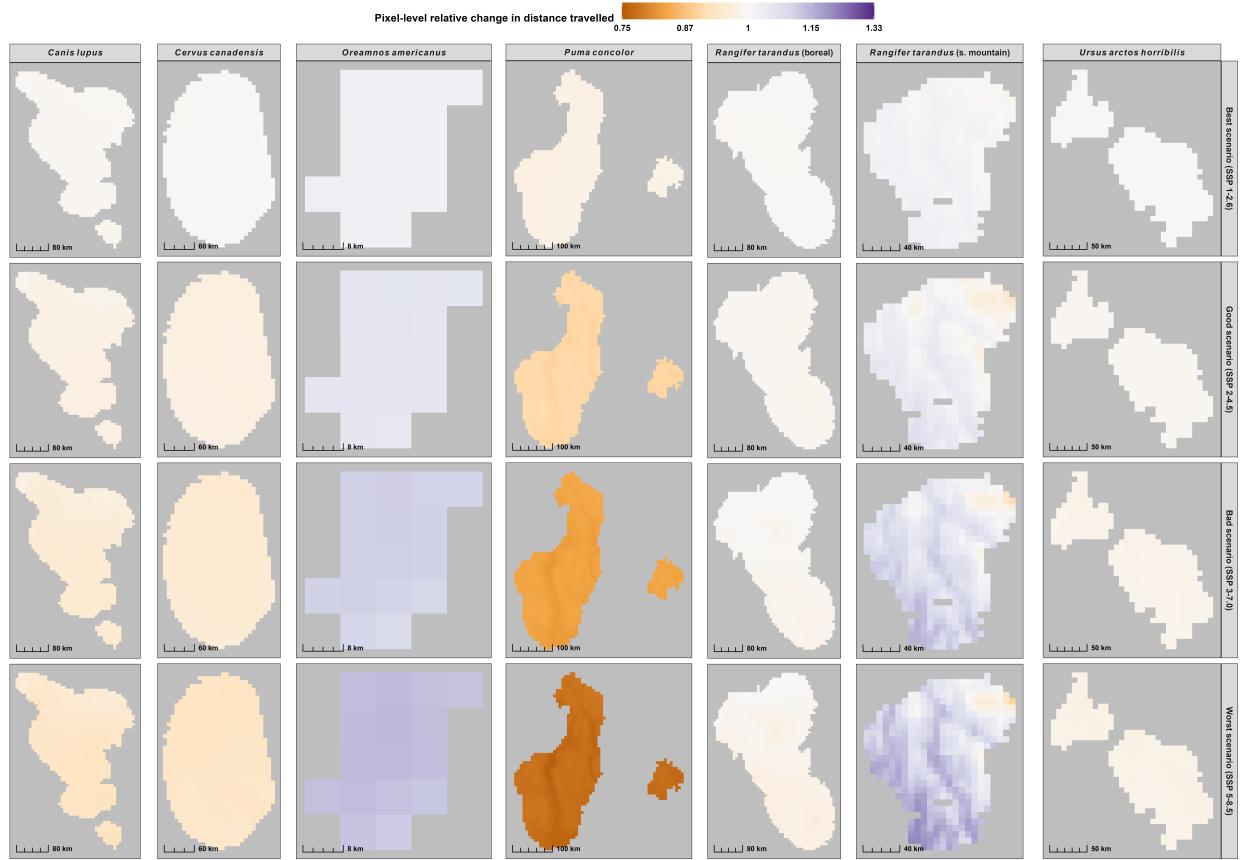


Figure 6: Climate change will impact each species' movement rates differently. The color scale indicates the predicted changes in distance traveled in 2100, relative to each pixel's average distance in 2025 across all four scenarios (i.e., not relative to other pixels). Values < 1 indicate a decrease, and values > 1 indicate an increase. For ease of readability, the color bar is on the \log_2 scale to help visualize patterns in doubling, and values are capped to 0.67 and 1.5 ($\approx 2^{0.585}$; original data ranged 0.50 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. All maps are shown with a BC Albers projection (EPSG:3005).

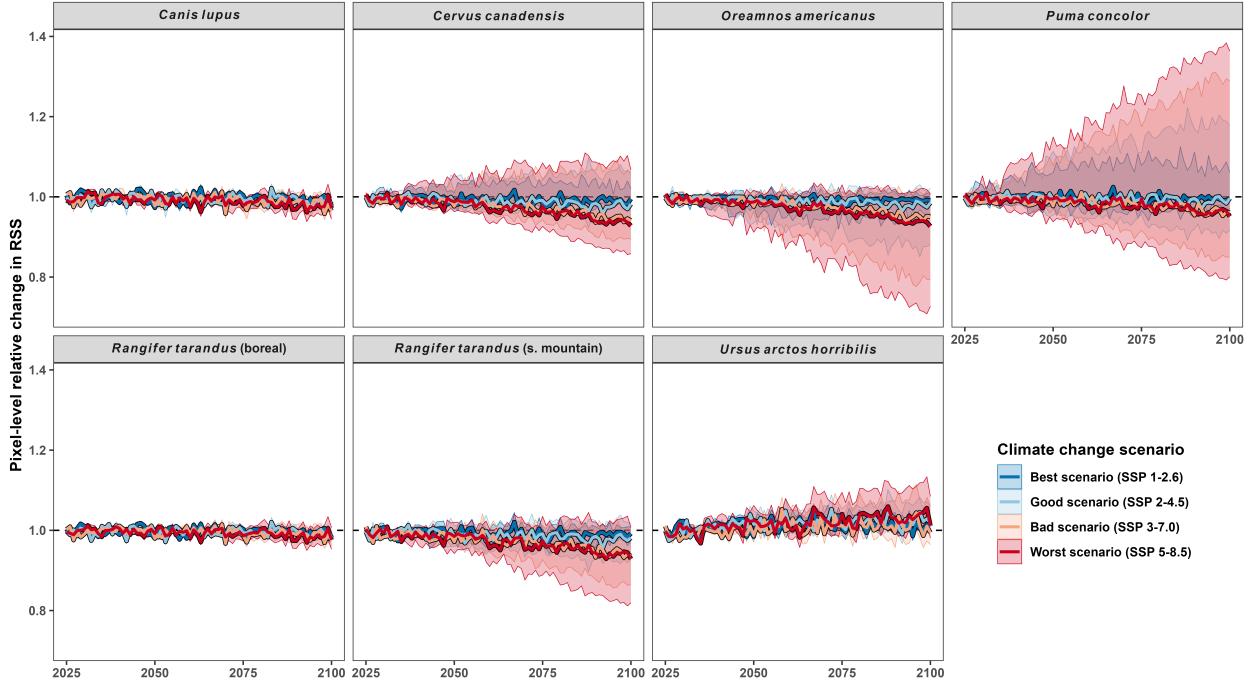


Figure 7: All species are expected to exhibit a decrease in median relative selection strength (RSS) for their current range, irrespective of climate change scenario, but decreases are stronger in the worse-case scenario. Lines indicate the projected change in median RSS within each species' observed extent within BC, 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).

358 5 Discussion

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

366 Predicting mammals' responses at the data-scarce fringes of the surface plots in Figs. 3
 367 and 4 comes with substantial uncertainty, particularly given that the responses are nonlinear.
 368 At warm temperatures, mammals (and other homeotherms) overheat (Alston *et al.*, 2020;
 369 Dyer *et al.*, 2023), so their movement behaviour and that of their competitors, predators,
 370 and/or prey can often be substantially different from the behaviour at typical temperatures.

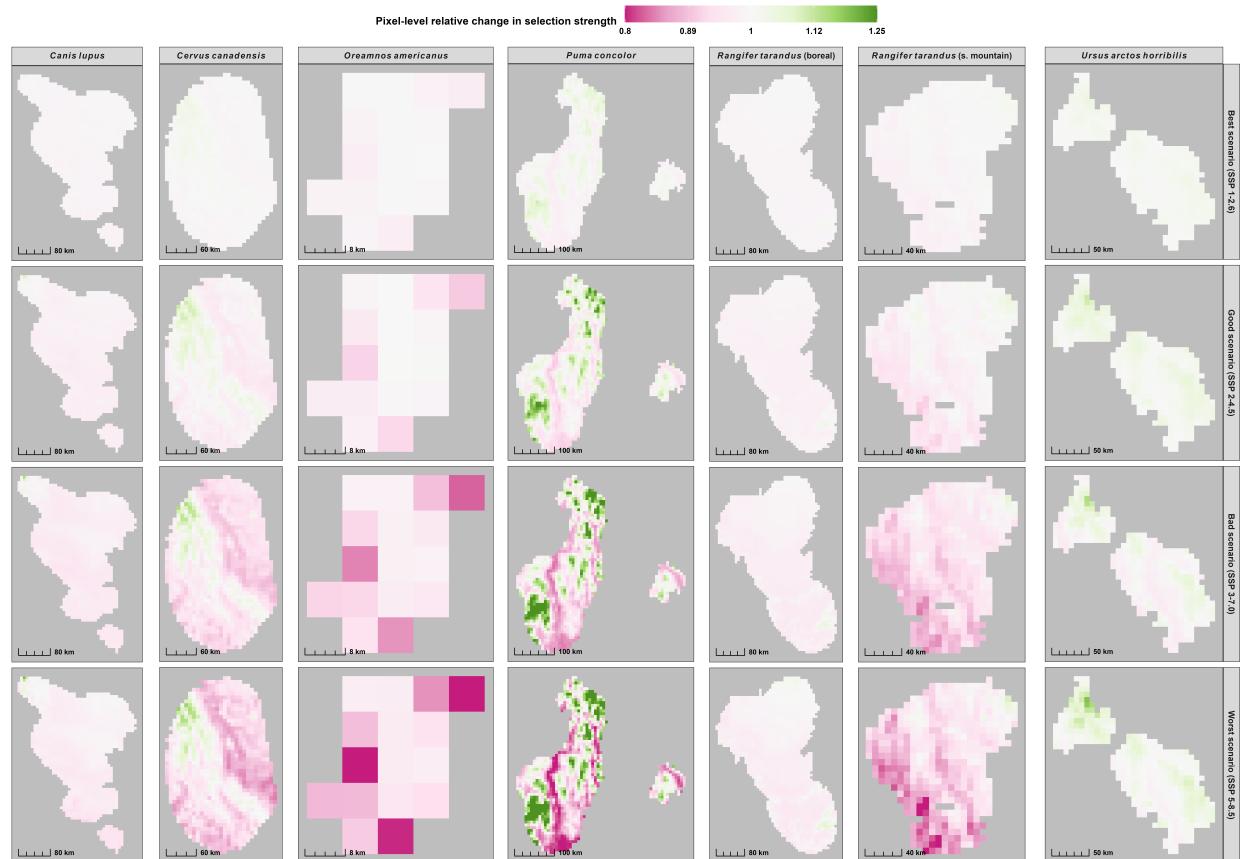


Figure 8: Climate change will impact each species' habitat relative selection strength (RSS) differently. The color scale indicates the predicted changes in RSS in 2100, relative to each location's average RSS in 2025 across all four scenarios (i.e., not relative to other pixels). Values < 1 indicate 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). All maps are shown with a BC Albers projection (EPSG:3005).

³⁷¹ As extreme temperature events become more frequent and prolonged throughout the year
³⁷² (Yao *et al.*, 2022; IPCC, 2023), mammals will be increasingly forced towards atypical be-
³⁷³ haviours that may alter community structures and behaviours, both during such events and
³⁷⁴ afterwards (Logares & Nuñez, 2012; Anderson *et al.*, 2017; Zhang *et al.*, 2023). For instance,
³⁷⁵ changes in climate and phenology impact the life history and behaviour of many hibernat-
³⁷⁶ ing mammals (Wells *et al.*, 2022), and hot weather can also affects mammals' sleep quality
³⁷⁷ (Mortlock *et al.*, 2024) and likelihood to enter torpor (Fjelldal *et al.*, 2021).

³⁷⁸ Changes in animal movement behavior may also alter the frequency and intensity of
³⁷⁹ human-wildlife conflict, especially with the addition of growing pressures from human de-
³⁸⁰ velopment and presence (Sih *et al.*, 2011; Johnson *et al.*, 2018; Weststrate *et al.*, 2024). At
³⁸¹ the same time, warmer winters may reduce mammals' energetic expenditure (Berger *et al.*,
³⁸² 2018; Schmidt *et al.*, 2020), increase ease of movement as snow cover and depth decrease
³⁸³ (Leclerc *et al.*, 2021; Melin *et al.*, 2023), increase their chances of finding food or being
³⁸⁴ preyed on (Gilbert *et al.*, 2017; Hou *et al.*, 2020; Pedersen *et al.*, 2021; Slatyer *et al.*, 2022;
³⁸⁵ Sullender *et al.*, 2023), and affect the timing and duration of migrations (Sawyer *et al.*, 2009;
³⁸⁶ Leclerc *et al.*, 2021; Xu *et al.*, 2021). These changes will likely have complex consequences
³⁸⁷ for population and ecosystem structures and dynamics as prey, predators, and competitors
³⁸⁸ experience altered seasonal cycles and increasingly common climate "weirding" (Bunnell *et*
³⁸⁹ *al.*, 2011).

³⁹⁰ Our ability to respond changes in climate is contingent on our ability to prepare for and
³⁹¹ predict change. However, predicting animal behaviour becomes increasingly complicated as
³⁹² the conditions animals are exposed to deviate from current, typical conditions, especially
³⁹³ when responses are nonlinear and data are sparse. Consequently, we do not present our re-
³⁹⁴ sults as a definitive guide to how mammals in western Canada will respond to climate change.
³⁹⁵ Instead, we hope they serve as a starting point to (1) demonstrate that mammals' movement
³⁹⁶ rates and habitat selection depend on temperature and (2) how one can estimate mammals'
³⁹⁷ changes in movement behaviour due to climate change. Additionally, communicating un-

certainty in one's estimates is crucial in assessing risk probabilistically, and appropriate measures of uncertainty require careful and robust modeling (Aven & Kvaløy, 2002; Ayre & Landis, 2012; Czado & Brechmann, 2014).

Achieving the “30 by 30” goal will require international collaboration (Huang & Zhai, 2021) as well as active partnership with local Peoples, especially Indigenous Peoples (Wong et al., 2020; Lamb et al., 2023). Understanding the consequences of climate change on mammals’ movement behaviour is a first step towards proactively responding to how mammals will respond to human-induced rapid environmental change (Sih et al., 2011; Williams & Blois, 2018). In the following sections, we discuss the implications of our results in more detail. We then expand on consequences for conservation during the 21st century and considerations for future studies.

5.1 Effects of temperature on movement rates

The heterogeneity mammals’ responses to temperature suggests that ecological communities will respond to change in complex and interconnected ways. Although our models do not account for explicit physiological or phenological changes, the surfaces in Fig. 3 suggest that warmer temperatures cause many species to alter their daily and seasonal activity patterns (most visible in cougars and grizzly bears). For example, when temperatures were above 0°C, cougars moved most at night, but when temperatures were below 0°C they tended to move more throughout the day. Throughout the year, they adapted their tolerance to temperature and moved less when it was relatively hot (for a given time of year), especially in spring and summer. The strong reduction in the mid-day movement rates of wolves, elk, cougars, and boreal caribou when summer temperatures were above 20°C suggests that the increasingly common and intense heat waves across western Canada will have community-wide impacts on movement rates, encounter rates, and potentially community structure (Martinez-Garcia et al., 2020). More work is necessary on quantifying interspecific responses to temperature, including the effects of temperature on predation rates (but see: Cunningham et al., 2021;

⁴²⁴ Glass *et al.*, 2021; Brivio *et al.*, 2024). The increase in intensity and frequency of extreme
⁴²⁵ heat events (Bunnell *et al.*, 2011; Yao *et al.*, 2022) will likely also impact the occurrence and
⁴²⁶ timing of hibernation (Wells *et al.*, 2022) and migration or seasonal range expansions (Morley,
⁴²⁷ 2021; Carbeck *et al.*, 2022; Malpeli, 2022). However, not all species may be able to adapt at
⁴²⁸ the current rate of climate change (Heten *et al.*, 2014; Williams & Blois, 2018), especially
⁴²⁹ since landscape changes will likely depend not only on the direct effect of temperature but
⁴³⁰ also on cascading changes in the availability and unpredictability of resources (McLellan &
⁴³¹ McLellan, 2015; Pigeon *et al.*, 2016; Mezzini *et al.*, 2025).

⁴³² 5.2 Effects of temperature on habitat selection

⁴³³ As with the effects of temperature on movement rates, the heterogeneity of temperature
⁴³⁴ effects on species' habitat selection indicates that efficient and proactive habitat conservation
⁴³⁵ will require taxonomic nuance. In particular, our HRSFs did not account for any explicit
⁴³⁶ physiological responses to temperature that may impact movement, such as changes in the
⁴³⁷ phenology of plants, fire, ice, or mammalian physiology (e.g., moulting, fat storages) or
⁴³⁸ behaviour (e.g., migration, food caching), other than as direct responses to temperature.
⁴³⁹ Consequently, the behavioural changes we present should be interpreted carefully. While
⁴⁴⁰ some seasonal cycles do not depend directly on temperature and may thus not be impacted
⁴⁴¹ directly by climate change (such as those driven by photoperiod, see Liu *et al.*, 2022), the
⁴⁴² predictions we present also rely on the assumption that mammals will not adapt these
⁴⁴³ seasonal cycles to temperature-dependent cues, such as weather (Xu & Si, 2019) or forage
⁴⁴⁴ availability (Middleton *et al.*, 2018), which may not be correct. Additionally, it is important
⁴⁴⁵ to stress the distinction between habitat selection and quality. While animals tend to select
⁴⁴⁶ for high-quality habitats (Kacelnik *et al.*, 1992; Wright, 2024), high selection strength can
⁴⁴⁷ also be a consequence of an ecological trap (Swearer *et al.*, 2021; Zuñiga-Palacios *et al.*,
⁴⁴⁸ 2021).

⁴⁴⁹ **5.3 Predicted changes in movement during the 21st century**

⁴⁵⁰ Achieving the goals laid out by the “30 by 30” conservation initiative (Convention on
⁴⁵¹ Biological Diversity, 2022) will require careful planning but often also rapid action. In the
⁴⁵² case of Canada, only 13.7% of its terrestrial areas and inland waters were protected at the
⁴⁵³ end of 2023 (Environment and Climate Change Canada, 2024; Minister of Environment
⁴⁵⁴ and Climate Change, 2024). Additionally, efficient and effective conservation will require
⁴⁵⁵ collaboration with Indigenous and local communities to ensure Treaties are respected in the
⁴⁵⁶ process (Turner & Clifton, 2009; Wong *et al.*, 2020; Falardeau *et al.*, 2022; Lamb *et al.*,
⁴⁵⁷ 2023) while also actively preparing for future change (Desjardins *et al.*, 2020; Hessami *et al.*,
⁴⁵⁸ 2021).

⁴⁵⁹ The diversity in predicted changes in movement behavior by 2100 (both across species
⁴⁶⁰ and within species’ current ranges) and high spatial heterogeneity in Fig. 8 highlight the
⁴⁶¹ need for careful planning that incorporates not only reliable estimates of change but also
⁴⁶² pragmatic and communicable measures of uncertainty and variability around such estimates.
⁴⁶³ For example, the width of the prediction intervals in Fig. 5 suggest that spatial and intra-
⁴⁶⁴ individual variation should be accounted for when deciding the location and size of protected
⁴⁶⁵ areas (Jeltsch *et al.*, 2025). Population-level means that ignore such variation can greatly
⁴⁶⁶ limit the efficacy of conservation projects (Muff *et al.*, 2020; Mortlock *et al.*, 2024; Silva
⁴⁶⁷ *et al.*, 2025). Additionally, accurate estimates of the effects of changes in temperature on
⁴⁶⁸ mammals’ movement require a holistic view of the direct effects of temperature on mammals’
⁴⁶⁹ movement directly as well as its effects on other drivers of movement, such as forage and prey
⁴⁷⁰ availability (Mezzini *et al.*, 2025), encounter rates (Hou *et al.*, 2020; Martinez-Garcia *et al.*,
⁴⁷¹ 2020), population dynamics (Smith *et al.*, 2023), competitive pressure (Tórrez-Herrera *et al.*,
⁴⁷² 2020), and predation risk (Kohl *et al.*, 2019). This complexity results in the great variation
⁴⁷³ among the responses of different species (and individuals), especially as populations undergo
⁴⁷⁴ a rapid cascade of change (Botero *et al.*, 2015) and animals face increasing pressures from
⁴⁷⁵ human activity, including habitat fragmentation, habitat loss, and greater human presence

⁴⁷⁶ in wild spaces (Sawyer *et al.*, 2009; Sih *et al.*, 2011; Tucker *et al.*, 2018; Rice, 2022; Rosenthal
⁴⁷⁷ *et al.*, 2022; Weststrate *et al.*, 2024). As selection strength for current ranges changes (and
⁴⁷⁸ likely decreases), some animals may disperse, relocate to a new habitat, or remain within
⁴⁷⁹ the current range despite the reduced fitness and increased extinction risk (Duncan *et al.*,
⁴⁸⁰ 2012; Logares & Nuñez, 2012; Anderson *et al.*, 2017).

⁴⁸¹ **5.4 Species-specific considerations**

⁴⁸² **5.4.1 *Canis lupus***

⁴⁸³ **5.4.2 *Cervus canadensis***

⁴⁸⁴ **5.4.3 *Oreamnos americanus***

⁴⁸⁵ **5.4.4 *Puma concolor***

⁴⁸⁶ attraction for disconnected patches of high elevation could lead to fragmentation or traps

⁴⁸⁷ **5.4.5 *Rangifer tarandus* (boreal)**

⁴⁸⁸ Increasing temperatures increased RSS for both elevations near ~500 m as well as > 1,000
⁴⁸⁹ m, but such a selection is only possible if: (1) such habitats exist in the animals' range, and
⁴⁹⁰ (2) crossing the 500 m to > 1,000 m regions is safe and attractive

⁴⁹¹ **5.4.6 *Rangifer tarandus* (s. mountain)**

⁴⁹² HRSFs do not account for migratory behavior due to reproduction or predation risk

⁴⁹³ **5.4.7 *Ursus arctos horribilis***

⁴⁹⁴ **5.5 Considerations for future studies**

⁴⁹⁵ Our work highlights three central considerations for future research: (1) telemetry sam-
⁴⁹⁶ pling rates should be designed primarily in relation to the movement timescales of the species

497 of interest (Noonan *et al.*, 2019a; Nathan *et al.*, 2022; Pease, 2024), (2) the number of indi-
498 viduals tracked and the length of each telemetry should depend not just on population size
499 but also the rate of environmental change, and (3) predicting changes in movement behaviour
500 becomes highly complex when responses are nonlinear, especially when changes depend on
501 many interacting factors (Polazzo *et al.*, 2024) and one is interested in predicting responses
502 in extreme conditions for which data are scarce (Steixner-Kumar & Gläscher, 2020).

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

524 areas and timescales, the model estimates are not independent of the scale of the sampling
525 frequency.

526 When landscapes are relatively predictable across years, a larger number of sampled
527 individuals is likely preferable over the duration of each tracking period. The greater number
528 of tracked animals allows one to quantify the variance across individuals, including the
529 range of conditions and environments that individual animals are in. A good estimate of
530 inter-individual variance provides better coefficient estimates along with more appropriate
531 measures of uncertainty. However, when conditions across years are stochastic, multi-year
532 telemetries allow one to better estimate inter-annual variation without conflating it with
533 inter-individual differences. Given the widespread, rapid, and accelerating changes across
534 many habitats (particularly at high elevations and at high latitudes), we suggest researchers
535 focus on long-term telemetry datasets to quantify the effects of intra-annual variability while
536 increasing the ranges of temperatures each individual is observed in. Longer observational
537 periods can also improve the chances of observing different community dynamics, such as
538 shifts in predator-prey dynamics.

539 Temperature affects many aspects of mammalian physiology and behavior, including en-
540 ergetics, sleep, and movement behavior. Climatic changes during the last two centuries have
541 exposed many mammals to novel and increasingly extreme environmental conditions that
542 have led to visible changes that impact not only individuals but also ecological and human
543 communities. However, quantifying the effects of climate change is often complex, espe-
544 cially as conditions become increasingly different and extreme events become increasingly
545 common. Accurately quantifying the nonlinear effects of temperature on when, how, and
546 where mammals move requires careful data collection and model design. We have presented
547 a multi-species analysis of the effects of temperature on mammalian movement rates and
548 habitat selection in hopes that other researchers can leverage this framework and models
549 to expand our understanding of how temperature affects the movement behavior of other
550 species, including smaller mammals, more elusive species, and non-mammal animals. Un-

derstanding of how temperature affects each species in a community will allow us to begin making community-level inferences of how temperature will affect intra-specific interactions from a movement behavior perspective (Nathan *et al.*, 2008, 2022; Martinez-Garcia *et al.*, 2020). While adopting such a perspective is surely not simple, it would result in more complete estimates of the effects of climate change on community ecology, particularly when species are exposed to rapid change in many important variables. Future work should explore the effects of temperature on movement behavior while accounting for finer-scale and species specific variables that were not accounted for in this study. Examples of these include temporally dynamic measures of forest type and age, canopy density, competitive pressures, forage availability, and predator avoidance, or environmental stochasticity. However, many of these data not available, so we also suggest that more work be done on quantifying such measures using spatiotemporally dynamic models and sufficiently fine resolutions.

6 Author contributions

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

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