

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 behaviour cycles. Consequently, it is still unclear how mammals will adapt their movement behaviour 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 behaviour and community structure will become crucial for effectively and proactively understanding mammalian movement behaviour 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 behaviour as a consequence
- ⁸ Gerlich *et al.* (2025)
- ⁹ • Walker *et al.* (2019): Global climate change and invariable photoperiods: {A} mismatch that jeopardizes animal fitness
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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; Merkle *et al.*, 2016; Mezzini *et al.*, 2025), optimize habitat use
¹⁸ (Schwerdt *et al.*, 2024; Winter *et al.*, 2024), and avoid predators and competitors (Tórrez-
¹⁹ Herrera *et al.*, 2020; Peterson *et al.*, 2021; Bartashevich *et al.*, 2024; Tan *et al.*, 2024).
²⁰ However, ambient temperature affects mammals' movement rates by altering the energetic
²¹ cost of movement (McNab, 1970; Taylor *et al.*, 1982; Brown *et al.*, 2004; Fuller *et al.*, 2016;
²² Jahn & Seebacher, 2022) and the risk of hyperthermia (Hetem *et al.*, 2014; Dyer *et al.*, 2023).
²³ Animals may search for a short-term buffer from extreme heat or cold via thermal refugia
²⁴ (Hannah *et al.*, 2014; Elmore *et al.*, 2017; Attias *et al.*, 2018; Arechavala-Lopez *et al.*, 2019;
²⁵ Gulland *et al.*, 2022), which may even be preferred over forage abundance (Hall *et al.*, 2016).
²⁶ By altering mammals' movement speed and habitat use (jointly, their movement behaviour:
²⁷ Nathan *et al.*, 2008, 2022), ambient temperature also affects the consequences of movement
²⁸ behaviour (Alston *et al.*, 2020; Giroux *et al.*, 2023), such as encounter rates with resources
²⁹ (Mezzini *et al.*, 2025), humans (Weststrate *et al.*, 2024), predators, prey, or competitors
³⁰ (Martinez-Garcia *et al.*, 2020; Glass *et al.*, 2021; Brivio *et al.*, 2024). Behavioural changes
³¹ to temperature are exacerbated in extreme cold (Wilson *et al.*, 2001; Berger *et al.*, 2018)
³² and extreme heat (Powers *et al.*, 2017; Alston *et al.*, 2020; Giroux *et al.*, 2023; Verzuh *et al.*,
³³ 2023).

³⁴ Mammals are particularly susceptible to adverse effects from excessive heat (Sherwood &
³⁵ Huber, 2010). While extreme cold often leads to reduced movement, provided that individ-
³⁶ uals can find refuge and take advantage of their body heat (Berger *et al.*, 2018; Hou *et al.*,
³⁷ 2020; Glass *et al.*, 2021), extreme heat can often result in more severe physiological damage
³⁸ in a shorter span of time (Jessen, 2001; Sherwood & Huber, 2010; Mota-Rojas *et al.*, 2021;
³⁹ Newediuk *et al.*, 2024). Due to mammals' difficulty at dissipating heat, particularly when

40 ambient temperatures are near or above their body temperature, they are particularly sen-
41 sitive to extreme heat, especially with increasing body size (Dyer *et al.*, 2023; Verzuh *et al.*,
42 2023). Furthermore, species that experience narrow temperature ranges (i.e., ‘temperature
43 specialists’) tend to be more sensitive to changes (e.g., giant anteaters, *Myrmecophaga tri-*
44 *dactyla*: Giroux *et al.*, 2023), while species that experience wide ranges of temperature vari-
45 ation (i.e., ‘temperature generalists’) can adapt more easily to change (Levins, 1974; Botero
46 *et al.*, 2015; Dupont *et al.*, 2024). Still, generalists’ greater adaptability is tested when they
47 are subject to changes that are more severe (McCain, 2019; Rantanen *et al.*, 2022), affect
48 many factors at once (e.g., temperature, snow depth, ecosystem phenology, and resource
49 availability: Polazzo *et al.*, 2024), or are too rapid and severe to respond within a lifetime
50 or a few generations (Levins, 1974; Fuller *et al.*, 2016; Xu *et al.*, 2021).

51 In the last century, many ecosystems experienced widespread warming that resulted in
52 milder and shorter winters, hotter and longer summers, and a greater risk of extremely high
53 temperatures (IPCC, 2023). As heat stress intensifies over the next 100 years, mammals will
54 continue to suffer impacts on their fitness, movement rates, and habitat selection (Deb *et*
55 *al.*, 2020; Woo-Durand *et al.*, 2020), which will be exacerbated by more frequent and intense
56 extreme events (Bunnell *et al.*, 2011) and anthropogenic habitat loss, modification, and frag-
57 mentation (Sawyer *et al.*, 2009; Sih *et al.*, 2011; Weststrate *et al.*, 2024). It remains unclear
58 how or whether species will be able to respond to climate change in the current century (Deb
59 *et al.*, 2020; Woo-Durand *et al.*, 2020; Verzuh *et al.*, 2023), especially if populations fail to
60 adapt to changes (Botero *et al.*, 2015; Sawyer *et al.*, 2019) or are physiologically incapable
61 to do so (Sherwood & Huber, 2010; Williams & Blois, 2018). Preparing for and responding
62 to future changes require a comprehensive understanding of how temperature will affect how
63 and where mammals move, as well as the implications such changes will have on species’
64 adaptability and overall community structure. Recent work has documented the effects of
65 climate change on mammals’ ranges (Leclerc *et al.*, 2021), movement behaviour (Melin *et al.*,
66 2023), thermoregulation (Mota-Rojas *et al.*, 2021), and trait-based responses (e.g., body size,

67 activity time, and elevational and latitudinal distribution McCain, 2019). However, there
68 remains a need for fine-scale estimates of the effects of temperature on mammals' movement
69 behaviour and quantitative predictions of how their behaviour will respond to climate change
70 in the current century (IPCC, 2023).

71 Western Canada is currently experiencing rapid widespread warming (Turner & Clifton,
72 2009; Kienzle, 2018; Dierauer *et al.*, 2021), phenological shifts (Kienzle, 2018; Basu *et al.*,
73 2024; Tysor, 2025), and more frequent and intense extreme events (Zhang *et al.*, 2023),
74 including forest fires (Zurowski, 2023). As we approach the deadline for the Kunming-
75 Montreal Global Biodiversity Framework (i.e., the “30 by 30” initiative), a global effort to
76 conserve 30% of the world’s lands and oceans by 2030 (Convention on Biological Diversity,
77 2022), Canadian decision makers must understand which areas will be of greatest value for
78 maximizing and protecting biodiversity not only for current conditions but future decades,
79 too. Failing to understand how climate change will affect mammalian movement behaviour
80 will hinder our ability to respond to the current climate crisis and make decisions that are
81 viable in the long term. Furthermore, understanding how temperature affects individual
82 species is the first step towards understanding how temperature impacts the community
83 dynamics (Hegel *et al.*, 2010) and habitat phenology (Bunnell *et al.*, 2011; Duncan *et al.*,
84 2012; Merkle *et al.*, 2016; Slatyer *et al.*, 2022).

85 In this paper, we quantify the effects of proximal air temperature on mammalian move-
86 ment behaviour, namely movement rates and habitat selection of six large-bodied terrestrial
87 mammal species in western Canada (wolves: *Canis lupus*, elk: *Cervus canadensis*, moun-
88 tain goats: *Oreamnos americanus*, cougars: *Puma concolor*, boreal and southern mountain
89 caribou: *Rangifer tarandus*, and grizzly bears: *Ursus arctos horribilis*; Table 1). Using over
90 25 years of telemetry data throughout a large spatial range of western Canada and hourly
91 air temperature data, we estimate how these mammals altered their probability of mov-
92 ing, speed when moving, and habitat selection in response to temperature. We then pair
93 the estimated responses with climate change projections to forecast the species’ movement

94 behaviour during the 21st century under different climate-change scenarios (referred to as
 95 Shared Socioeconomic Pathways, SSP, Riahi *et al.*, 2017). We discuss the consequences of
 96 these changes in movement behaviour at the individual, population, and community levels.
 97 We also provide directions for future research and solutions for overcoming some common
 98 data limitations.

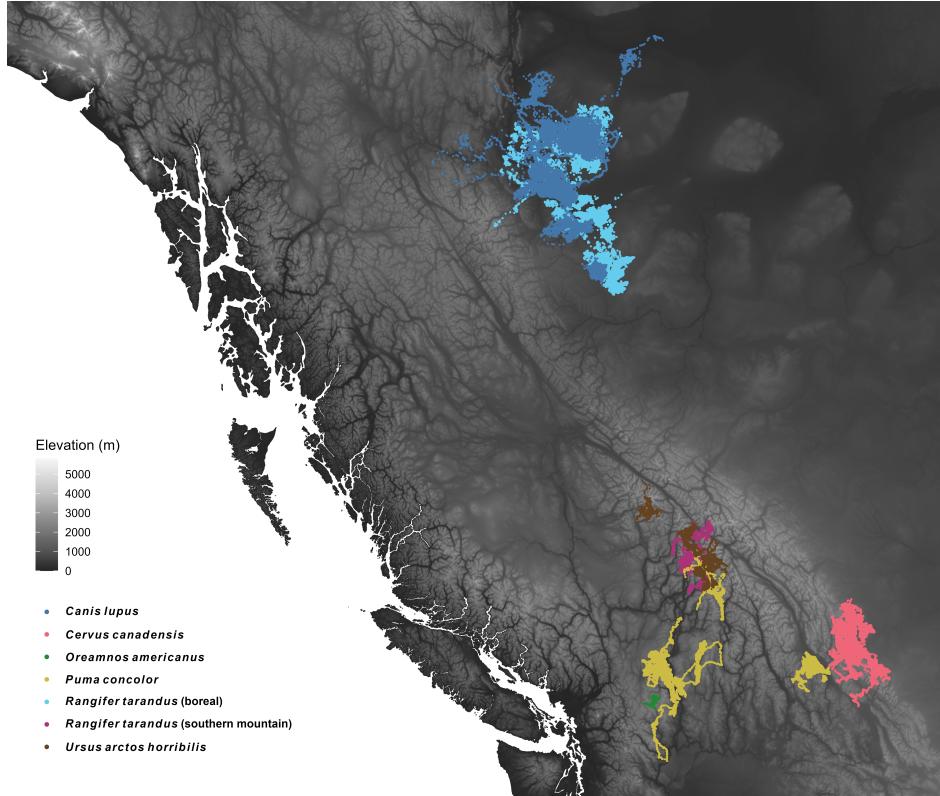


Figure 1: GPS telemetry data for the six species in this study (dots) over a digital elevation model for the study area.

Table 1: Summary statistics of each species' set of GPS data, including: the start and end of each set of GPS telemtries, the median sampling interval (Δt ; stratified by animal), number of animals (Animals), and number of animals with finite speed estimates (Has speed).

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

Species	Start	End	Δt (hours)	Animals	Has speed
<i>Ursus arctos horribilis</i>	2004-09-30	2009-09-07	1.00	18	18

99 3 Methods

100 3.1 Datasets used

101 This study leverages four main datasets: (1) a multi-species collection of GPS telemetry
 102 data (Fig. 1); (2) historical hourly air temperature from the ERA5 reanalyzed dataset (Euro-
 103 pean Center for Medium-range Weather Forecasting; Hersbach *et al.*, 2023); (3) temporally
 104 static rasters of percent forest cover, elevation, and distance from water; and (4) climate
 105 change projections under four Shared Socioeconomic Pathways (SSPs; Riahi *et al.*, 2017).

106 While we acknowledge there are other important variables (e.g., forest type, structure, and
 107 age; terrain slope and aspect), we limited our models to only use three simple variables
 108 for the sake of parsimony and comparability across species. See the discussion section for
 109 additional detail on the advantages and limitations of using such simple models.

110 3.1.1 GPS telemetry data

111 Elk (*Cervus canadensis*) data from Ciuti *et al.* (2012) were downloaded from Movebank
 112 (study name: Elk in southwestern Alberta, see Kays *et al.*, 2022). Boreal caribou (*Rangifer*
 113 *tarandus*) and wolf (*Canis lupus*) telemtries were acquired from a data repository of the
 114 British Columbia Oil and Gas Research and Innovation Society (BC OGRIS) that was col-
 115 lected as part of the boreal caribou radio-collaring program of the BC OGRIS Research
 116 and Effectiveness Monitoring Board (REMB; BC OGRIS, 2018). **MISSING INFO ON**
 117 **OTHER TELEMETRY DATA.** From the full set of telemetry data, we removed a total
 118 of 2396 problematic GPS locations (0.16%, including collar calibration data) after inspect-
 119 ing diagnostic plots of (1) distance from the median location, (2) straight-line displacement
 120 between locations, (3) turning angle, and (4) time interval between consecutive points. Par-

121 ticular attention was paid to points with large turning angles ($\gtrsim 170^\circ$) and excessively high
122 straight-line displacement, especially if antecedent and subsequent points indicated relatively
123 stationary behaviour (Appendix A).

124 3.1.2 Historical temperature data and climate change projections

125 Rasters of hourly reanalyzed air temperature data were downloaded from the ERA5 database
126 (Hersbach *et al.*, 2023) from the European Center for Medium-range Weather Forecasting
127 server (ECMWF; www.ecmwf.int; <https://cds.climate.copernicus.eu>). Proximal air temper-
128 ature was estimated for each location by extracting the value from the corresponding raster
129 cell from the temporally nearest raster using the `extract()` function from the `terra` package
130 (v. 1.7-46, Hijmans, 2023) for `R` (R Core Team, 2024).

131 We used the the `climatenetR` package (v. 1.0, Burnett, 2023) for `R` and `ClimateNA` (v.
132 7.4.2; Wang *et al.*, 2016; Mahony *et al.*, 2022) to obtain projected average monthly temper-
133 atures from 2020 to 2100 at a 0.08° spatial resolution. Since the climate projections only
134 provided monthly means and ranges but no measures of variance or distributional assump-
135 tions, we used the historical data for western Canada from 1998 to 2023 (extremes included)
136 to estimate the monthly variation in temperature, which we defined as σ_T^2 , the variance at
137 location $\langle x, y \rangle$ in month m for each year (e.g., the variance at coordinates $\langle -119.40, 49.94 \rangle$
138 in April 2005). We then modeled the estimated variance using a Generalized Additive Model
139 for Location and Scale (GAMLS, Rigby & Stasinopoulos, 2005; Stasinopoulos & Rigby, 2007;
140 section 7.9 in Wood, 2017) using the `mgcv` package for `R` (v. 1.9-1, Wood, 2017). The linear
141 predictor for the location (i.e., the mean) included smooth terms of: each year's estimated
142 within-pixel monthly mean temperature ($\hat{\mu}_T$), month (m), a two-dimensional smooth of spa-
143 tial coordinates $\langle x, y \rangle$, and a tensor product interaction term of month and space to allow
144 for seasonal terms to vary smoothly over space. The linear predictor for the scale term,
145 which governs the mean-variance relationship (table 3.1 on p. 104 of Wood, 2017), included
146 smooth terms of the monthly mean temperature, month, and space. We did not include

¹⁴⁷ smooth terms of year to avoid unrealistic projections when extrapolating beyond 2023.

¹⁴⁸ The model was thus

$$\begin{cases} \sigma_T^2 \sim \text{Gamma}(\mu_{\sigma_T^2}, \nu_{\sigma_T^2}) \\ \mathbb{E}(\sigma_T^2) = \mu_{\sigma_T^2} \\ \mathbb{V}(\sigma_T^2) = (\mu_{\sigma_T^2})^2 / \nu_{\sigma_T^2} \\ \log(\mu_{\sigma^2}) = \beta_{L,0} + f_{L,1}(\mu_T) + f_{L,2}(m) + f_{L,3}(x, y) + f_{L,4}(x, y, m) \\ \log(\nu_{\sigma^2}) = \beta_{S,0} + f_{S,1}(\mu_T) + f_{S,2}(m) + f_{S,3}(x, y) \end{cases}, \quad (1)$$

¹⁴⁹ where $\mu_{\sigma_T^2}$ and $\nu_{\sigma_T^2}$ indicate the location and scale parameters of the gamma distribution of
¹⁵⁰ σ_T^2 , and together they determine the variance of σ_T^2 , indicated as $\mathbb{V}(\sigma_T^2)$. Functions $f_{L,j}$ and
¹⁵¹ $f_{S,j}$ indicate the j^{th} smooth functions for the location and scale parameters, respectively.

¹⁵² To ensure the smooth functions of month, $f_{L,2}(m)$ and $f_{S,2}(m)$, joined smoothly between
¹⁵³ December and January, the terms use cyclic cubic spline bases. The spatial terms used two-
¹⁵⁴ dimensional Duchon splines, a generalization of thin-plate regression splines (p. 221 of Wood
¹⁵⁵ (2017)). The smoothness parameters were estimated via REstricted Maximum Likelihood
¹⁵⁶ (REML; p. 83 of Wood, 2017). See the Data Availability Statement for additional information
¹⁵⁷ on the code used to fit the model.

¹⁵⁸ We simulated hourly variation in future years by assuming hourly temperature followed
¹⁵⁹ a normal distribution with mean specified by the monthly `climatenar` climate projections
¹⁶⁰ and variance as specified by the gamma GMLS. For each month within each year from
¹⁶¹ 2025 to 2100, we simulated hourly weather by including temperatures from the 0.1 to the
¹⁶² 0.9 quantiles by increments of 0.1, and we weighted each quantile proportionally to the
¹⁶³ (normalized) Gaussian probability density for each quantile.

¹⁶⁴ **3.1.3 Resource rasters**

¹⁶⁵ We estimated percent forest cover and distance from water using the rasters created by
¹⁶⁶ Tuanmu & Jetz (2014). We calculated total forest cover by summing the temporally
¹⁶⁷ static rasters of evergreen/deciduous needle-leaf trees, evergreen broadleaf trees, deciduous
¹⁶⁸ broadleaf trees, and mixed/other trees (raster classes 1-4, respectively). We converted the
¹⁶⁹ raster of percent cover of open water (class 12) to a binary raster of pixels with water
¹⁷⁰ (cover > 0%) or without water (cover = 0%) and then calculated each pixel's distance
¹⁷¹ from the nearest pixel with water using the `distance()` function from the `terra` package.
¹⁷² Finally, we obtained two digital elevation models using the `get_elev_raster()` function
¹⁷³ from the `elevatr` package (v. 0.99.0, Hollister *et al.*, 2023). We used a raster with a zoom
¹⁷⁴ of 6 (a resolution of 0.009°) for model fitting and one with a zoom of 3 (a resolution of
¹⁷⁵ 0.08°) for downloading climate change projections via `climatenar`. All final rasters and
¹⁷⁶ code are available in the GitHub repository associated with this manuscript (see the Data
¹⁷⁷ Availability Statement).

¹⁷⁸ **3.2 Estimating mammals' instantaneous speeds**

¹⁷⁹ We modeled each animal's movement using continuous-time movement models (Fleming
¹⁸⁰ *et al.*, 2014) via the `ctmm` package (v. 1.2.0, Fleming & Calabrese, 2023) for `R`. We then
¹⁸¹ estimated each mammal's instantaneous speed at each observed location by applying the
¹⁸² `ctmm::speeds()` function on all models with finite speed estimates (415 of 433, Fleming *et*
¹⁸³ *al.*, 2014; Noonan *et al.*, 2019a). The 18 animals with insufficiently fine sampling to support
¹⁸⁴ movement models with finite speed were for one mountain goat, 15 boreal caribou, and two
¹⁸⁵ southern mountain caribou (Table 1).

¹⁸⁶ Since `ctmm`'s movement models assume a single moving state with stochastic but non-
¹⁸⁷ zero speed, we corrected data-informed speeds so that the minimum instantaneous speed
¹⁸⁸ could be 0. We performed this correction by subtracting each model's mean speed while
¹⁸⁹ assuming speeds were χ^2 -distributed. The function we used is available on GitHub (see the

190 Data Availability Statement). To avoid artifacts due to excessively small, non-zero speeds,
191 we determined whether an animal was moving or not using a k -means algorithm with 2
192 clusters for each species' distribution of detrended speeds. When the algorithm clearly failed
193 to discriminate between states, we estimated the split point using the inflection points in
194 histograms of the detrended speeds (Fig. B1).

195 **3.3 Estimating the effects of temperature on mammals' movement behaviour**

196 Ambient temperature is only one of the many drivers of mammalian movement behaviour
197 (Fig. 2). Many species adapt their movement rates (e.g., movement frequency and speed)
198 daily or seasonally in response to factors such as solar time, photoperiod, forage availability,
199 reproductive cycles, and predator avoidance. Similarly, ambient temperature also fluctuates
200 throughout the day and across seasons. Therefore, estimating the effects of temperature
201 on movement rates requires accounting for how mammals' response to temperature changes
202 with time of day and day of year (Fig. 2A; Péron *et al.*, 2017; Buderman *et al.*, 2018; Leclerc
203 *et al.*, 2021; Xu *et al.*, 2021). Similarly, mammals' selection strength for resources depends
204 on ambient temperature, since higher temperatures can promote a selection for refuge from
205 heat (e.g., thicker forest cover, higher elevation, proximity to water; Attias *et al.*, 2018;
206 Giroux *et al.*, 2023).

207 The two following sections detail the statistical framework and models we used to estimate
208 the effect on temperature on the six species' movement behavior. To assess the importance of
209 including temperature as an explicit covariate (as opposed to including its effects with time
210 of day and day of year), we fit models with and without smooth effects of temperature and
211 compared the fits of the two sets of models via analyses of deviance (a form of generalized
212 likelihood ratio tests) following the methods of Section 3.3 in Wood (2017). See Appendix
213 B for additional information.

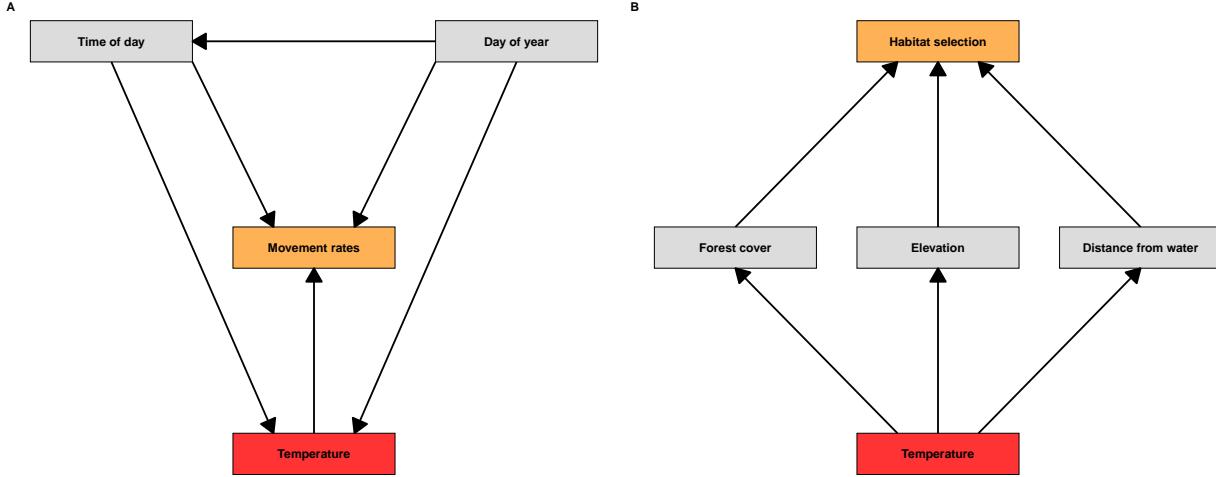


Figure 2: Directed Acyclical Graphs (DAGs) assumed for inferring the causal effects of temperature on each species' movement behaviour. (A) Ambient temperature affects mammals' movement rates (i.e. probability of moving, speed when moving, and distance traveled), but temperature is influenced by time of day and day of year. Additionally, the effects of temperature on movement rates depend on time of day and season, since animals may respond to temperatures differently at different times of day and or days of year. Finally, the effect of time of day changes seasonally due to changes in photoperiod. (B) Similarly, habitat selection depends on the availability and selection of resources (forest cover, elevation, and distance from water), but the selection strength for each resource is conditional on temperature. For example, an animal may avoid forested areas unless it is seeking refuge from extreme temperatures.

214 3.3.1 Effects of temperature on movement rates

215 We estimated the effects of temperature on mammals' instantaneous movement state (mov-
 216 ing or not) and speed when moving using two Hierarchical Generalized Additive Models
 217 (HGAMs, see Pedersen *et al.*, 2019 and Appendix B) with the `mgcv` package for R. The first
 218 HGAM estimated the probability that an animal was moving, $P(M)$, with a binomial fam-
 219 ily of distributions and logit link function. The second HGAM estimated an animal's speed
 220 when moving with a gamma family of distributions and log link function. We fit the models
 221 with fast Restricted Maximum Likelihood ('fREML') and discretized covariates (`discrete =`
 222 `TRUE`) to optimize computational efficiency with no appreciable losses to model performance
 223 (Appendix B; Wood *et al.*, 2015, 2017; Li & Wood, 2020). Together, the binomial HGAM
 224 and the gamma HGAM inform us on an animal's long-term average speed, since it is the
 225 product of the probability of moving and its average speed when moving.

226 The HGAMs (equations (2) and (3)) included fixed-effect intercepts for each species
 227 (β_s), random intercepts for each animal (Z_a), and species-level `by` smooths that allowed
 228 independent smoothness parameters for each species (model I in Figure 4 of Pedersen *et*

229 *al.*, 2019). The `by` smooths accounted for trends in time of day (in Pacific Daylight Time;
 230 `tod_pdt`), day of year (`doy`), and temperature (`temp_c`). To account for the cyclicity of time
 231 of day and day of year, the smooth terms used cyclic cubic splines (p. 202 of Wood, 2017).
 232 The models also had three tensor product interaction terms `by` each species: (1) day of year
 233 and time of day, (2) temperature and time of day, and (3) temperature and day of year. These
 234 three terms accounted for smooth changes in: (1) daily behavior across day of year, (2) the
 235 response to temperature over time of day (e.g., changes in nocturnality), and (3) the response
 236 to temperature over day of year (e.g., changes in coats and migration timing). Finally, two
 237 smooth terms of log-transformed sampling interval (`dt`; hours) corrected for biases in speed
 238 estimates arising from irregular GPS sampling intervals, since longer intervals result in lower
 239 speed estimates (Nathan *et al.*, 2022; DeNicola *et al.*, 2025). A global smooth term of $\log(dt)$
 240 accounted for the overall effect of sampling interval, while a factor-smooth interaction term
 241 (`bs = 'fs'`) of $\log(dt)$ and species accounted for species-level deviations from the global
 242 term while assuming a common smoothness parameter across species (model GS in Figure 4
 243 of Pedersen *et al.*, 2019). Formally, the model for movement state M , with $M = 0$ indicating
 244 no movement and $M = 1$ indicating movement, was

$$\left\{ \begin{array}{l} M \sim \text{Bin}(p) \\ \mathbb{E}(M) = p \\ \mathbb{V}(M) = p(1-p) \\ \text{logit}(p) = \beta_s + Z_a + f_{1,s}(\text{tod_pdt}) + f_{2,s}(\text{doy}) + f_{3,s}(\text{temp_c}) + \\ f_{4,s}(\text{doy}, \text{tod_pdt}) + f_{5,s}(\text{temp_c}, \text{tod_pdt}) + f_{6,s}(\text{temp_c}, \text{doy}) + \\ f_7(\log(dt)) + f_{8,s}(\log(dt)) \end{array} \right. , \quad (2)$$

245 while the model for movement speed when moving (i.e., $M = 1$, indicated with S) was

$$\left\{ \begin{array}{l} S \sim \text{Gamma}(\mu_S, \nu_S) \\ \mathbb{E}(S) = \mu_S \\ \mathbb{V}(S) = \mu_S^2 / \nu_S \\ \log(\mu_S) = \beta_s + Z_a + f_{1,s}(\text{tod_pdt}) + f_{2,s}(\text{doy}) + f_{3,s}(\text{temp_c}) + \\ f_{4,s}(\text{doy}, \text{tod_pdt}) + f_{5,s}(\text{temp_c}, \text{tod_pdt}) + f_{6,s}(\text{temp_c}, \text{doy}) + \\ f_7(\log(\text{dt})) + f_{8,s}(\log(\text{dt})) \end{array} \right. . \quad (3)$$

²⁴⁶ In both models, β_s indicates a fixed intercept for species s , Z_a indicates a Gaussian random
²⁴⁷ effect for animal a (of species s), $f_{j,s}$ indicates the j^{th} smooth function for species s , and
²⁴⁸ functions with two variables indicate tensor product interaction terms. The model code used
²⁴⁹ to fit the models is available in Appendix B.

²⁵⁰ **3.3.2 Effects of temperature on habitat selection**

²⁵¹ We estimated the effects of temperature on each species' selection for percent forest cover
²⁵² (`forest_perc`), elevation (`elevation_m`), and distance from water (`dist_water_m`) by fit-
²⁵³ ting a Hierarchical Resource Selection Function (HRSF) for each species. We fit each HRSF
²⁵⁴ using an HGAM with a Poisson family of distributions and log link function (Appendix B;
²⁵⁵ Aarts *et al.*, 2008). After removing non-resident individuals (Table B1), we accounted for the
²⁵⁶ spatiotemporal autocorrelation in the telemetry locations by weighting each point based on
²⁵⁷ the telemetry's Autocorrelated Kernel Density Estimate (Fleming & Calabrese, 2017; Noo-
²⁵⁸ nan *et al.*, 2019b; Alston *et al.*, 2022) to produce estimates of second-order habitat selection
²⁵⁹ (Johnson, 1980). Quadrature points were determined using the raster cells in each animal's
²⁶⁰ 99.9% AKDE percentile and given a weight of 1. The number of quadrature locations greatly
²⁶¹ outnumbered the number of observed locations (Fig. B12), especially after accounting for
²⁶² the AKDE weights (Fig. B13).

263 Each species' model had the same structure:

$$\left\{ \begin{array}{l} C \sim \text{Pois}(\lambda) \\ \mathbb{E}(C) = \mathbb{V}(C) = \lambda \\ \log(\lambda) = f_1(\text{forest_perc}) + f_2(\text{elevation_m}) + f_3(\text{dist_water_m}) + \\ Z_a + f_{4,a}(\text{forest_perc}) + f_{5,a}(\text{elevation_m}) + f_{6,a}(\text{dist_water_m}) + \\ f_7(\text{forest_perc}, \text{temp_c}) + f_8(\text{elevation_m}, \text{temp_c}) + \\ f_9(\text{dist_water_m}, \text{temp_c}) + f_{10}(\text{temp_c}) + f_{11,a}(\text{temp_c})) \end{array} \right. , \quad (4)$$

264 where O indicates whether an animal was observed ($O = 1$) or not ($O = 0$), and the species-
265 level indices are omitted for readability, but each term in the model can be assumed to be
266 species-specific. Smooth effects of percent forest cover (`forest_perc`), elevation (`elev_m`),
267 and distance to water (`dist_water_m`) accounted for the species-level selection strength
268 for each resource. A Gaussian random effect for each individual animal (Z_a) corrected for
269 uneven sampling across individuals, while factor-smooth interaction terms for each animal
270 ($f_{j,a}$) accounted for animal-level resource selection (i.e., individual-level deviations from the
271 species-level estimate; Jeltsch *et al.*, 2025). Tensor product interaction terms of the three
272 resources and temperature (`temp_c`) estimated the smooth change in resource selection at
273 different temperatures. Finally, marginal smooth terms of temperature and factor-smooth
274 interaction terms of temperature and animal accounted for species- and individual-level
275 sampling biases at different temperatures (e.g., sampling more during warm periods).

276 4 Results

277 Overall, 2.6% of GPS locations had temperatures lower than -20°C , while 6.5% had tem-
278 peratures above 20°C , and temperature ranges differed across species (Table 2, Fig. B2).
279 Sampling interval affected estimates of probability as well of as speed when moving (Fig.

280 B8). Consequently, we present all results while predicting specifically for one-hour sam-
 281 pling intervals. At 0°C, species differed in mean probabilities of moving ($\hat{P}(M)$; range:
 282 0.05 – 0.31), mean speed when moving ($\hat{\mathbb{E}}(S|M = 1)$; range: 0.42 – 2.67 km/h), and mean
 283 distance traveled (i.e., $\hat{P}(M) \times \hat{\mathbb{E}}(S|M = 1)$, range: 0.04 – 0.61 km/h; Table 2). Griz-
 284 zly bears had the lowest movement frequency ($\hat{P}(M) \approx 0.05$), while wolves and cougars
 285 moved most often ($\hat{P}(M) \geq 0.22$). Mountain goats and southern mountain caribou moved
 286 the slowest ($\hat{\mathbb{E}}(S|M = 1) \approx 0.43$ km/h), while wolves had the highest mean speed when
 287 moving ($\hat{\mathbb{E}}(S|M = 1) \approx 2.67$ km/h). Consequently, at 0°C, wolves traveled an average of
 288 0.22×2.67 km/h ≈ 0.6 km/h; 2.5 to 16.7 times further than other species.

Table 2: Summary statistics for the observed temperatures and estimated mean movement rates at °C. The second and third columns indicate the percentage of GPS locations (after data cleaning) with temperature (T) below -20°C and above 20°C, respectively. The subsequent columns indicate the estimated mean probability of moving ($\hat{P}(M = 1)$), mean speed when moving ($\hat{\mathbb{E}}(S)$; km/h), and mean distance travelled ($\hat{P}(M = 1) \times \hat{\mathbb{E}}(S) = \hat{\mathbb{E}}(D)$; km/h) as estimated by models without and with temperature (i.e., (...| T)), for a sampling interval of 1 hour and a temperature of $T = 0^\circ\text{C}$.

Species	$\hat{P}(M = 1)$							
	T < -20°C	T > +20°C	1)	$\hat{P}(M = 1 T)$	$\hat{\mathbb{E}}(S)$	$\hat{\mathbb{E}}(S T)$	$\hat{\mathbb{E}}(D)$	$\hat{\mathbb{E}}(D T)$
<i>C. canadensis</i>	1.7 %	13.0 %	0.16	0.17	0.57	0.57	0.09	0.10
<i>Canis lupus</i>	2.4 %	4.9 %	0.23	0.22	2.64	2.67	0.61	0.60
<i>O. americanus</i>	0.7 %	2.8 %	0.15	0.13	0.43	0.42	0.06	0.06
<i>P. concolor</i>	0.7 %	6.9 %	0.27	0.31	0.74	0.76	0.20	0.24
<i>R. tarandus;</i> <i>b</i>	6.8 %	7.9 %	0.19	0.18	0.71	0.73	0.14	0.13
<i>R. tarandus;</i> <i>sm</i>	1.3 %	3.4 %	0.11	0.11	0.43	0.42	0.05	0.05
<i>U. arctos h.</i>	0.0 %	8.4 %	0.05	0.05	0.72	0.72	0.04	0.04
Total	2.6 %	6.5 %						

289 Across all species, Relative Selection Strength (RSS) was weakest for forest cover and
 290 strongest for elevation. At temperatures near 0°C, wolves selected for forest cover ($\gtrsim 50\%$),
 291 elevations near 1 km, and distances from water < 5 km; elk selected for intermediate forest
 292 cover ($\approx 50\%$), elevations between 1 and 2 km, and distances from water of 10-15 km;
 293 mountain goats selected for sparse forest cover (< 25%), elevations near 1.5 km, and distances
 294 from water < 5 km; cougars selected for dense forest cover ($> 75\%$), an elevation of ~ 1 km,

and distances from water < 7.5 km; boreal caribou selected for forest cover between 50% and 75%, 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 \lesssim 5 km; and grizzly bears selected for relatively sparse forest cover (25-50%), elevation between 1 and 2 km, and distances from water < 3 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 p-values $< 2.2 \times 10^{-16}$; all $\Delta AIC \geq 342$; Table B2 and subsequent pages in Appendix B). Accounting for temperature even 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.

4.1 Effects of temperature on movement rates

Species' changes in movement rates to temperature varied in both direction and magnitude (Figs. 3, B4-B6), even after accounting for differences in daily and seasonal activity (e.g., sleeping, migration, hibernation; Figs. B4-B6). Smooth interaction terms were well-behaved and indicated clear shifts in activity over time of day and day of year for all species. The models had good in-sample prediction (Fig. B7) and explained reasonably high proportions of the deviance (79.3% for the gamma model and 10.7% for the binomial model, which is relatively high for a binomial model with binary responses: see ch. 11 of McElreath, 2020). All species adapted their daily and seasonal movement behaviour to changes in temperature (Fig. 3). The clearest example of this was cougars. In late spring (June 1st), they moved from evening to early morning if temperatures were below 20°C, but if temperatures were above 20°C they moved mostly between 3:00 and 6:00 AM. Throughout the year, they tended to move more when it was colder, but what they perceived as "colder" was relative to the time of year. All species' estimated probability of moving and speed when moving decreased with sampling intervals above 1 hour, except for cougars' speed, although the estimated

321 trends were highly uncertain (Fig. B8). Uncertainties around the estimated effects were
 322 generally higher at extreme temperatures due to lower data availability (Figs. B4A, B5A,
 323 and B6A).

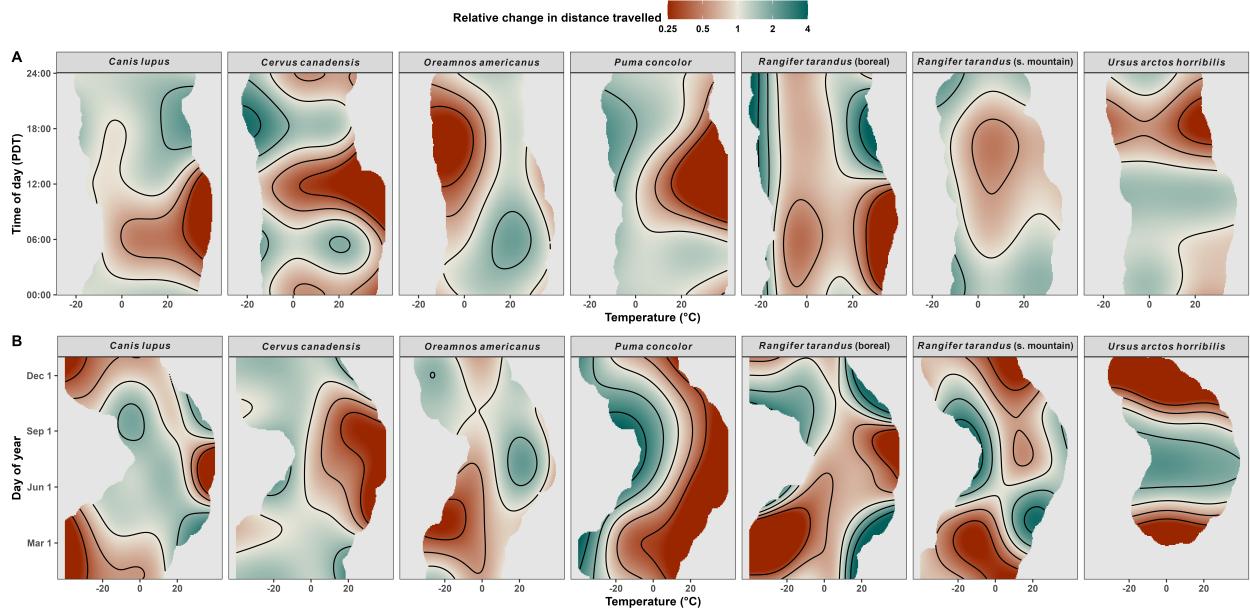


Figure 3: **Temperature is a strong determinant of how far and when mammals travel.** The fill indicates the effects of temperature on the relative change in distance travelled (probability of moving times mean speed when moving) over time of day on June 1st (**A**) and day of year at 12:00 PDT (**B**).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

324 4.2 Effects of temperature on habitat selection

325 Species' RSS was generally strongest for elevation and weakest for forest cover, but RSS
 326 depended significantly on temperature for all species (all p-values $< 2.2 \times 10^{-16}$; Fig. 4).
 327 Changes in RSS with temperature were strongest for elevation and generally weakest for
 328 distance from water, but there were no common trends across all species for any of the
 329 three resources. All species, with the exception of cougars, exhibited clear temperature-
 330 dependent shifts in their preference for forest cover. At higher temperatures, wolves relaxed
 331 their preference for forested areas, while mountain goats relaxed their preference open areas
 332 (cover < 50%). As temperatures warmed, elk and boreal caribou shifted towards more forest
 333 cover closer to 50%, while southern mountain caribou and grizzly bears selected for areas
 334 with 50% forest cover or less. All species shifted elevationally with temperature, although

boreal caribou ha a much sharper change in RSS across elevation. Elk, mountain goats, and cougars increased in elevation with temperature, while wolves, southern mountain caribou, and grizzly bears decreased in elevation. Wolves, elk, and southern mountain caribou moved closer to water with temperature, while mountain goats, cougars, and grizzly bears moved somewhat further away from water but remained mainly within 5-10 of water. As with movement rates, estimated RSS was generally most uncertain at extreme temperatures, for which data was scarcer (Fig. B15).

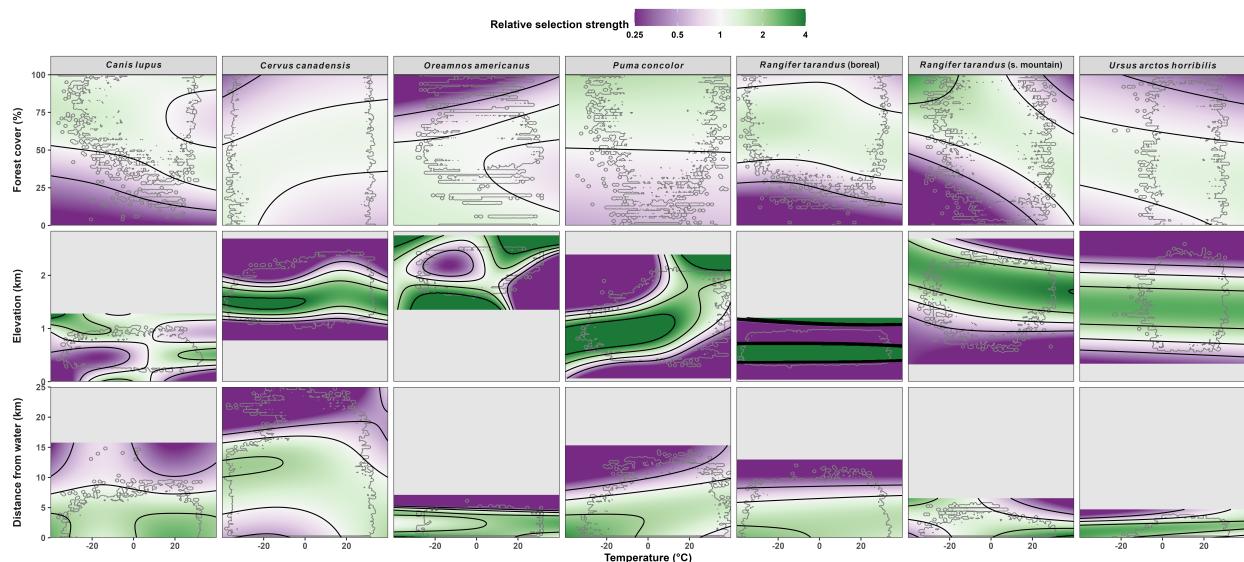


Figure 4: Mammals' habitat selection depends on ambient temperature. Estimated relative selection strength (RSS) for forest cover (%), elevation (km), and distance from water (km) as a function of temperature. The grey contours indicate the extent of each species' observed data. RSS values were re-centered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

4.3 Predicted changes in movement behaviour during the 21st century

Predicted changes in movement rates with future climate change varied across species in both magnitude and direction, but worse SSPs always corresponded to greater absolute changes (Fig. 5). Additionally, species that were predicted to move less often did not necessarily have lower speeds when moving, and vice versa (Figs. B9 and B10). Absolute relative changes in distance travelled were small under the best-case SSP (0-4% change in 2100 relative to 2025). Under the worst-case SSP, absolute changes by 2100 (relative to 2025) ranged from ~2% (grizzly bears) to ~24% (cougars). Notably, while the models estimated that grizzly bears would move substantially less (if at all) in late fall and winter (Figs. 3, B4), the models

351 did not explicitly account for changes in hibernation phenology. Consequently, the climate
 352 change projections do not explicitly account for changes in energetic needs or physiology.
 353 Projected changes in 2100 varied spatially due to spatial heterogeneity in climate change
 354 projections (Fig. 6). Again, absolute changes were generally greatest under worse SSPs, but
 355 the direction of change at each location also varied across SSPs (most visible in cougars).

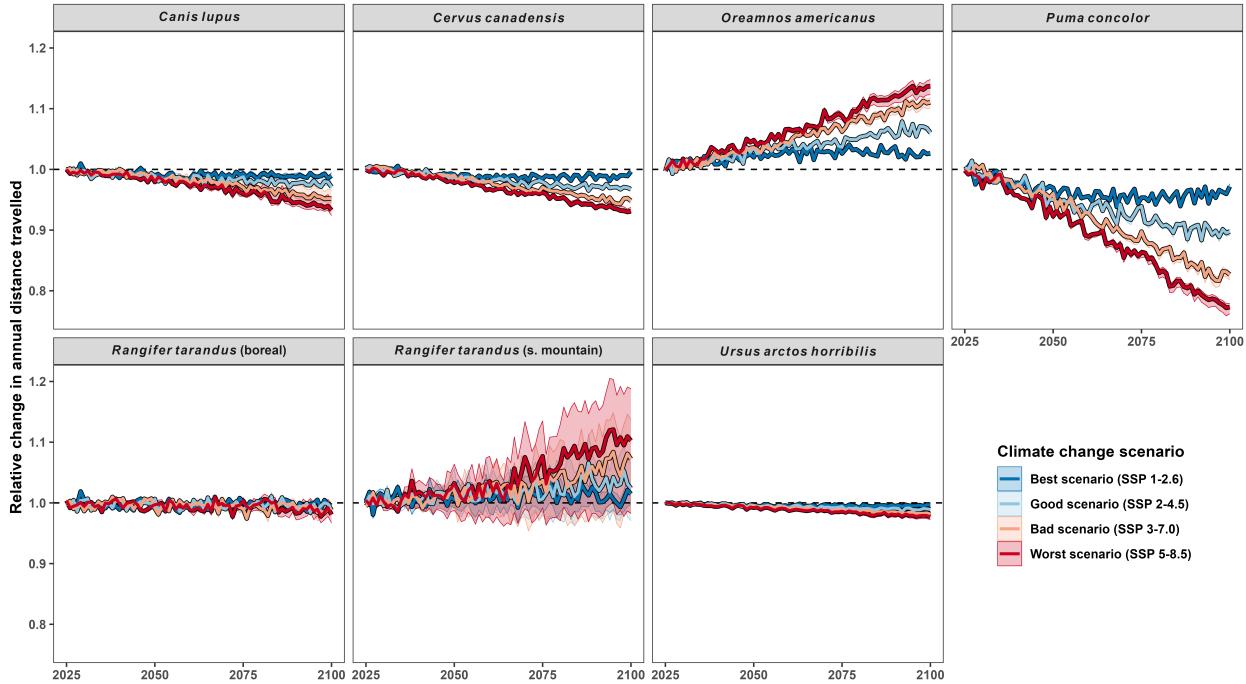


Figure 5: Species will adapt their movement rates differently in response to climate change, but worse climate-change scenarios will result in the greatest change. Bold lines indicate the median change in distance travelled (probability of moving times speed when moving) due to predicted changes in temperature within each species' observed extent. Shaded areas indicate the 95th and 5th percentiles. Changes are relative to the mean predicted distance travelled at each location in 2025, averaged across the four Shared Socioeconomic Pathways (SSPs). Values > 1 indicate an increase, while values < 1 indicate a decrease. The projections only account for changes in movement frequency and speed, and they ignore changes in physiology or movement costs.

356 Median RSS was projected to decrease over time within the each species' observed range,
 357 but, again, changes were stronger under worse SSPs (Fig. 7). Decreases were most pro-
 358 nounced in areas with the lowest RSS and most severe for elk, mountain goats, pumas, and
 359 southern mountain caribou. Changes for boreal wolves and caribou were relatively negli-
 360 gible. Elk, cougars, and grizzly bears were predicted to increase their selection strength
 361 for top-RSS areas, and elk, mountain goats, cougars, and southern mountain caribou were
 362 predicted to further decrease their selection for areas with low RSS. Unsurprisingly, the
 363 change in RSS between 2025 and 2100 also varied spatially for all species (Fig. 8). Overall,

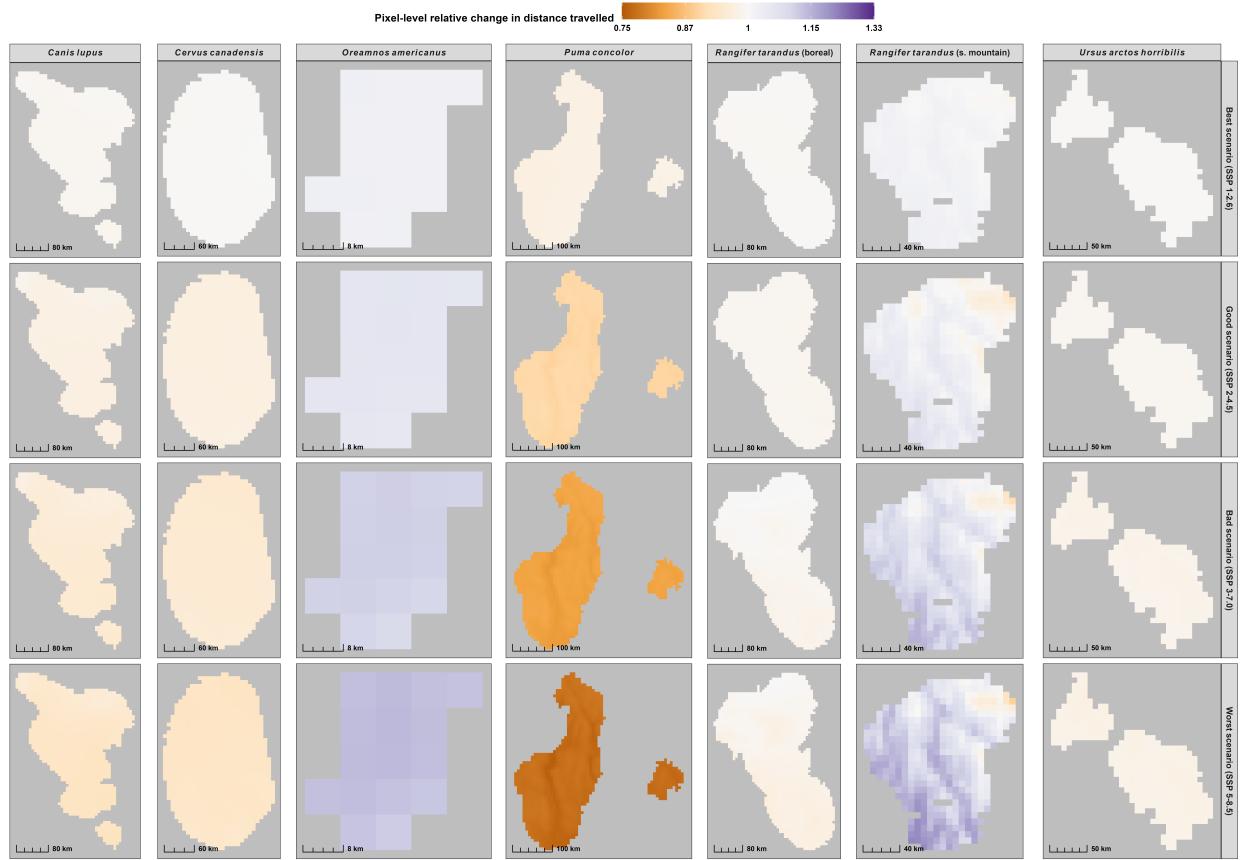


Figure 6: **Climate change will impact each species' movement rates differently, but changes will also vary spatially.** The color of each pixel indicates the predicted changes in distance traveled in 2100 at that pixel, relative to the value in 2025, averaged across all four scenarios. Values < 1 indicate 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). The predictions only account for the predicted temperature throughout the areas and ignore environmental factors such as terrain slope, soil type, and forest density. All maps are shown in the BC Albers Equal Area Conic projection (EPSG:3005).

364 RSS decreased throughout most of each species' current range, although elk, cougars, and
 365 bears were predicted to increase their selection for higher-altitude habitats. Still, none of
 366 the species were projected to increase RSS throughout their habitat (9).

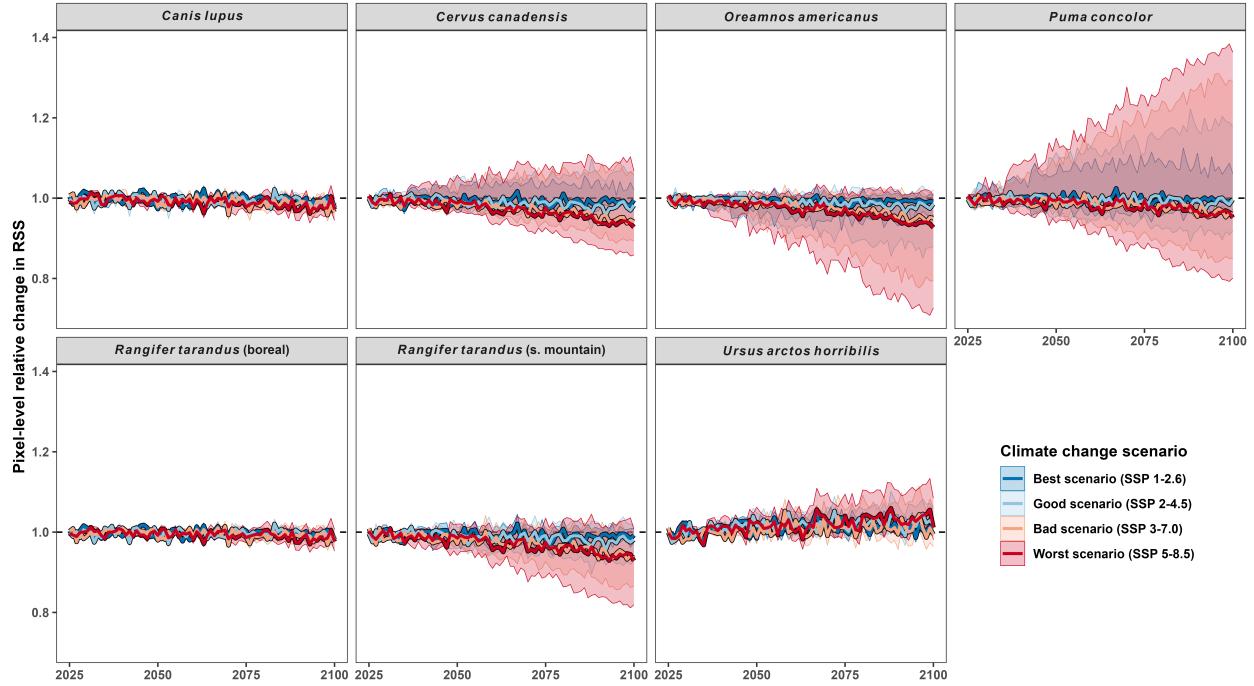


Figure 7: Species will adapt their habitat selection differently in response to climate change, but worse climate-change scenarios will result in the greatest change. Bold lines indicate the change in median RSS due to predicted changes in temperature within each species' observed extent. Shaded areas indicate the 95th and 5th percentiles in change in RSS. Values > 1 indicate an increase, while values < 1 indicate a decrease. Changes are relative to each location's mean RSS in 2025, averaged across the four Shared Socioeconomic Pathways (SSPs).

367 5 Discussion

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

375 Predicting mammals' responses at the data-scarce fringes of the surface plots in Figs. 3

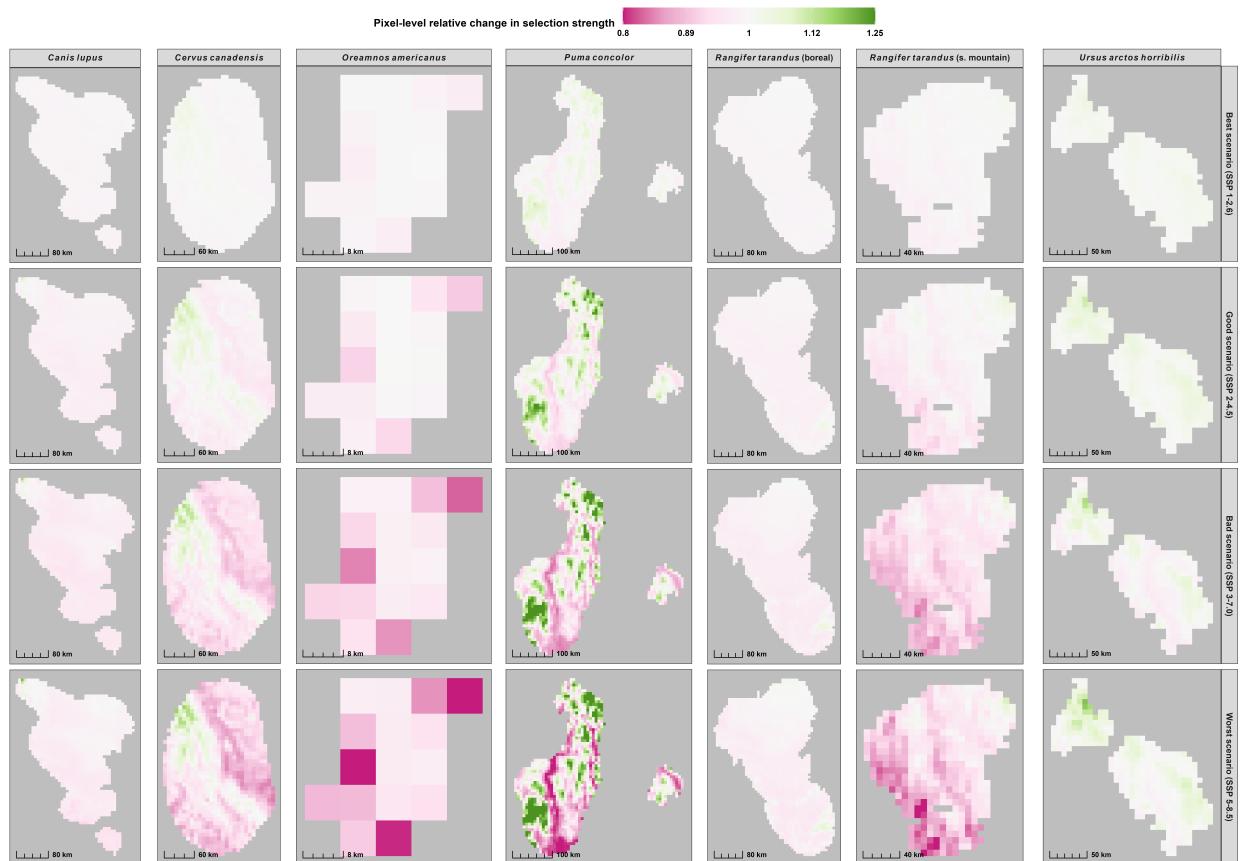


Figure 8: Climate change will impact each species' relative selection strength (RSS) differently. The color scale indicates the predicted changes in RSS in 2100, relative to each location's average RSS in 2025 across all four scenarios (i.e., not relative to other pixels). Values < 1 indicate a decrease 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 0.8 and 1.25 ($\approx 2^{\pm 0.322}$; original data ranged 0.71 to 1.93). All maps are shown in the BC Albers Equal Area Conic projection (EPSG:3005).

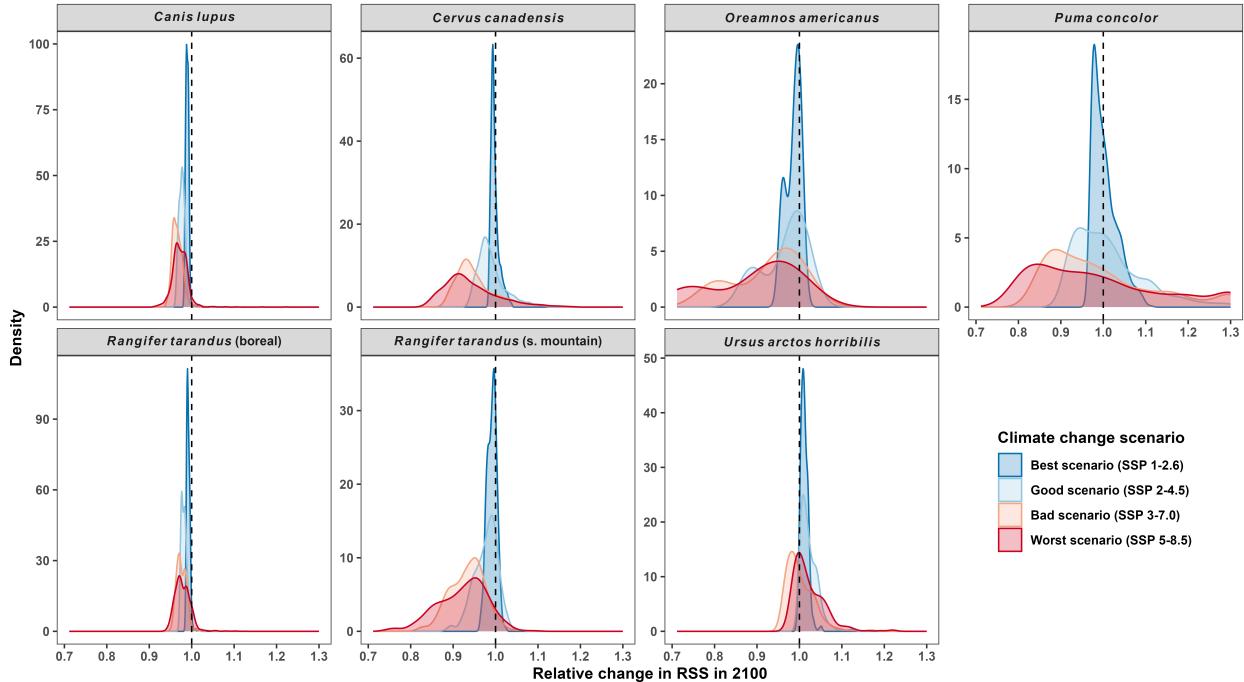


Figure 9: Climate change will cause species to decrease their selection strength for their current habitats, but worse climate change scenarios will have the greatest impact. The density plots indicate each species' change in RSS in 2100 for their current habitat (Fig. 8), relative to each location's RSS in 2025. Values < 1 indicate a decrease and values > 1 indicate an increase. For ease of readability, values > 1.3 were changed to 1.3 (original maximum: 1.93).

and 4 comes with substantial uncertainty, particularly given that the responses are nonlinear. At warm temperatures, mammals (and other homeotherms) overheat (Alston *et al.*, 2020; Dyer *et al.*, 2023), so their movement behaviour and that of their competitors, predators, and/or prey can often be substantially different from the behaviour at typical temperatures. As extreme temperature events become more frequent and prolonged throughout the year (Yao *et al.*, 2022; IPCC, 2023), mammals will be increasingly forced towards atypical behaviours that may alter community structures and behaviours, both during such events and afterwards (Logares & Nuñez, 2012; Anderson *et al.*, 2017; Zhang *et al.*, 2023). For instance, changes in climate and phenology impact the life history and behaviour of many hibernating mammals (Wells *et al.*, 2022), and hot weather can also affects mammals' sleep quality (Mortlock *et al.*, 2024) and likelihood to enter torpor (Fjelldal *et al.*, 2021). Changes in animal movement behaviour may also alter the frequency and intensity of human-wildlife conflict, especially with the addition of growing pressures from human development and presence (Sih *et al.*, 2011; Johnson *et al.*, 2018; Weststrate *et al.*, 2024). At

390 the same time, warmer winters may reduce mammals' energetic expenditure (Berger *et al.*,
391 2018; Schmidt *et al.*, 2020), increase ease of movement as snow cover and depth decrease
392 (Leclerc *et al.*, 2021; Melin *et al.*, 2023), increase their chances of finding food or being
393 preyed on (Gilbert *et al.*, 2017; Hou *et al.*, 2020; Pedersen *et al.*, 2021; Slatyer *et al.*, 2022;
394 Sullender *et al.*, 2023), and affect the timing and duration of migrations (Sawyer *et al.*, 2009;
395 Leclerc *et al.*, 2021; Xu *et al.*, 2021). These changes will likely have complex consequences
396 for population and ecosystem structures and dynamics as prey, predators, and competitors
397 experience altered seasonal cycles and increasingly common climate "weirding" (Bunnell *et*
398 *al.*, 2011).

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

410 *Achieving the "30 by 30" goal will require international collaboration (Huang & Zhai,
411 2021) as well as active partnership with local Peoples, especially Indigenous Peoples (Wong
412 et al., 2020; Lamb et al., 2023). Understanding the consequences of climate change on mam-
413 mals' movement behaviour is a first step towards proactively responding to how mammals will
414 respond to human-induced rapid environmental change (Sih et al., 2011; Williams & Blois,
415 2018). In the following sections, we discuss the implications of our results in more detail.
416 We then expand on consequences for conservation during the 21st century and considerations*

⁴¹⁷ for future studies.

⁴¹⁸ 5.1 Effects of temperature on movement rates

⁴¹⁹ The heterogeneity mammals' responses to temperature suggests that ecological communities
⁴²⁰ will respond to change in complex and interconnected ways. Although our models do not
⁴²¹ account for explicit physiological or phenological changes, the surfaces in Fig. 3 suggest that
⁴²² warmer temperatures cause many species to alter their daily and seasonal activity patterns
⁴²³ (most visible in cougars and grizzly bears). For example, when temperatures were above 0°C,
⁴²⁴ cougars moved most at night, but when temperatures were below 0°C they tended to move
⁴²⁵ more throughout the day. Throughout the year, they adapted their tolerance to temperature
⁴²⁶ and moved less when it was relatively hot (for a given time of year), especially in spring and
⁴²⁷ summer. The strong reduction in the mid-day movement rates of wolves, elk, cougars, and
⁴²⁸ boreal caribou when summer temperatures were above 20°C suggests that the increasingly
⁴²⁹ common and intense heat waves across western Canada will have community-wide impacts
⁴³⁰ on movement rates, encounter rates, and potentially community structure (Martinez-Garcia
⁴³¹ *et al.*, 2020). More work is necessary on quantifying interspecific responses to temperature,
⁴³² including the effects of temperature on predation rates (but see: Cunningham *et al.*, 2021;
⁴³³ Glass *et al.*, 2021; Brivio *et al.*, 2024). The increase in intensity and frequency of extreme
⁴³⁴ heat events (Bunnell *et al.*, 2011; Yao *et al.*, 2022) will likely also impact the occurrence and
⁴³⁵ timing of hibernation (Wells *et al.*, 2022) and migration or seasonal range expansions (Morley,
⁴³⁶ 2021; Carbeck *et al.*, 2022; Malpeli, 2022). However, not all species may be able to adapt at
⁴³⁷ the current rate of climate change (Hatem *et al.*, 2014; Williams & Blois, 2018), especially
⁴³⁸ since landscape changes will likely depend not only on the direct effect of temperature but
⁴³⁹ also on cascading changes in the availability and unpredictability of resources (McLellan &
⁴⁴⁰ McLellan, 2015; Pigeon *et al.*, 2016; Mezzini *et al.*, 2025).

441 5.2 Effects of temperature on habitat selection

442 *Overall, estimated selection strength was weakest for forest cover and*
443 *strongest for elevation. Elevation is the only raster that doesn't change no-*
444 *ticeably over time, so time-varying rasters of the other two would have likely*
445 *given stronger (and better) estimates.*

446 As with the effects of temperature on movement rates, the heterogeneity of temperature
447 effects on species' habitat selection indicates that efficient and proactive habitat conservation
448 will require taxonomic nuance. In particular, our HRSFs did not account for any explicit
449 physiological responses to temperature that may impact movement, such as changes in the
450 phenology of plants, fire, ice, or mammalian physiology (e.g., moulting, fat storages) or
451 behaviour (e.g., migration, food caching), other than as direct responses to temperature.
452 Consequently, the behavioural changes we present should be interpreted carefully. While
453 some seasonal cycles do not depend directly on temperature and may thus not be impacted
454 directly by climate change (such as those driven by photoperiod, see Liu *et al.*, 2022), the
455 predictions we present also rely on the assumption that mammals will not adapt these
456 seasonal cycles to temperature-dependent cues, such as weather (Xu & Si, 2019) or forage
457 availability (Middleton *et al.*, 2018), which may not be correct. Additionally, it is important
458 to stress the distinction between habitat selection and quality. While animals tend to select
459 for high-quality habitats (Kacelnik *et al.*, 1992; Wright, 2024), high selection strength can
460 also be a consequence of an ecological trap (Swearer *et al.*, 2021; Zuñiga-Palacios *et al.*,
461 2021).

- 462 • geographic space *sensu* Matthiopoulos (2022)
463 • environmental space *sensu* Matthiopoulos (2022)
464 • G space is the realization of the theoretical E space

465 **5.3 Predicted changes in movement during the 21st century**

466 Achieving the goals laid out by the “30 by 30” conservation initiative (Convention on
467 Biological Diversity, 2022) will require careful planning but often also rapid action. In the
468 case of Canada, only 13.7% of its terrestrial areas and inland waters were protected at the
469 end of 2023 (Environment and Climate Change Canada, 2024; Minister of Environment
470 and Climate Change, 2024). Additionally, efficient and effective conservation will require
471 collaboration with Indigenous and local communities to ensure Treaties are respected in the
472 process (Turner & Clifton, 2009; Wong *et al.*, 2020; Falardeau *et al.*, 2022; Lamb *et al.*,
473 2023) while also actively preparing for future change (Desjardins *et al.*, 2020; Hessami *et al.*,
474 2021).

475 The diversity in predicted changes in movement behaviour by 2100 (both across species
476 and within species’ current ranges) and high spatial heterogeneity in Fig. 8 highlight the
477 need for careful planning that incorporates not only reliable estimates of change but also
478 pragmatic and communicable measures of uncertainty and variability around such estimates.
479 For example, the width of the prediction intervals in Fig. 5 suggest that spatial and intra-
480 individual variation should be accounted for when deciding the location and size of protected
481 areas (Jeltsch *et al.*, 2025). Population-level means that ignore such variation can greatly
482 limit the efficacy of conservation projects (Muff *et al.*, 2020; Mortlock *et al.*, 2024; Silva
483 *et al.*, 2025). Additionally, accurate estimates of the effects of changes in temperature on
484 mammals’ movement require a holistic view of the direct effects of temperature on mammals’
485 movement directly as well as its effects on other drivers of movement, such as forage and prey
486 availability (Mezzini *et al.*, 2025), encounter rates (Hou *et al.*, 2020; Martinez-Garcia *et al.*,
487 2020), population dynamics (Smith *et al.*, 2023), competitive pressure (Tórrez-Herrera *et al.*,
488 2020), and predation risk (Kohl *et al.*, 2019). This complexity results in the great variation
489 among the responses of different species (and individuals), especially as populations undergo
490 a rapid cascade of change (Botero *et al.*, 2015) and animals face increasing pressures from
491 human activity, including habitat fragmentation, habitat loss, and greater human presence

492 in wild spaces (Sawyer *et al.*, 2009; Sih *et al.*, 2011; Tucker *et al.*, 2018; Rice, 2022; Rosenthal
493 *et al.*, 2022; Weststrate *et al.*, 2024). As selection strength for current ranges changes (and
494 likely decreases), some animals may disperse, relocate to a new habitat, or remain within
495 the current range despite the reduced fitness and increased extinction risk (Duncan *et al.*,
496 2012; Logares & Nuñez, 2012; Anderson *et al.*, 2017).

497 **5.4 Species-specific considerations**

498 **5.4.1 *Canis lupus***

499 **5.4.2 *Cervus canadensis***

500 **5.4.3 *Oreamnos americanus***

501 **5.4.4 *Puma concolor***

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

503 **5.4.5 *Rangifer tarandus* (boreal)**

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

507 **5.4.6 *Rangifer tarandus* (s. mountain)**

508 HRSFs do not account for migratory behaviour due to reproduction or predation risk

509 **5.4.7 *Ursus arctos horribilis***

510 **5.5 Considerations for future studies**

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

513 of interest (Noonan *et al.*, 2019a; Nathan *et al.*, 2022; Pease, 2024), (2) the number of in-
514 dividuals tracked and the duration of each telemetry should depend not just on population
515 size but also the rate of environmental change, and (3) predicting changes in movement
516 behaviour becomes highly complex when responses are nonlinear, especially when changes
517 depend on many interacting factors (Polazzo *et al.*, 2024) and one is interested in predict-
518 ing responses in extreme conditions for which data are scarce (Steixner-Kumar & Gläscher,
519 2020).

520 While the `ctmm` movement models produced scale-independent estimates of speed (i.e.,
521 model interpretation is independent of sampling interval: Noonan *et al.*, 2019a), the accu-
522 racy, size, and stability of speed estimates still depended on the GPS sampling frequency.
523 This dependency is because coarsely-sampled movement data contains information on large-
524 scale movements (range crossings, migrations) but not fine-scale movements, including first-
525 order habitat selection (Johnson, 1980). Using the boreal caribou as an example, the 13-hour
526 sampling interval allows us to reasonably estimate the caribou's movement path at a tempo-
527 ral scale of approximately 13 hours (or greater), but we cannot produce reasonable movement
528 trajectories at a much finer (e.g., hourly) scale. Nathan *et al.* (2022) provides additional
529 examples of how the frequency of location data affects the results that can be inferred by
530 modeling movement behaviour. Consequently, we suggest being cautious when comparing
531 estimated movement behaviours across species, even though all predictions have been cor-
532 rected to the hourly timescale by predicting for 1-hour time intervals (i.e., `dt_hours = 1`).
533 Ideally, sampling schedules should be fine enough to reconstruct animals' movement move-
534 ment paths. Good estimates of an animal's speed and trajectory require telemetry locations
535 to be taken more often than the animal's directional persistence (Noonan *et al.*, 2019a), so
536 that, on average, the dataset contains multiple locations in between changes in direction.
537 What constitutes a change in direction depends on what movement scale one is investigating.
538 Small-scale movements and first-order spatial selection will require more frequent sampling
539 than migratory movement or second-order and third-order spatial selection. While `ctmm`

540 movement models are scale-invariant in that any model can be scaled to larger or smaller
541 areas and timescales, the model estimates are not independent of the scale of the sampling
542 frequency.

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

556 Temperature affects many aspects of mammalian physiology and behaviour, including
557 energetics, sleep, and movement behaviour. Climatic changes during the last two centuries
558 have exposed many mammals to novel and increasingly extreme environmental conditions
559 that have led to visible changes that impact not only individuals but also ecological and
560 human communities. However, quantifying the effects of climate change is often complex,
561 especially as conditions become increasingly different and extreme events become increas-
562 ingly common. Accurately quantifying the nonlinear effects of temperature on when, how,
563 and where mammals move requires careful data collection and model design. We have pre-
564 sented a multi-species analysis of the effects of temperature on mammalian movement rates
565 and habitat selection in hopes that other researchers can leverage this framework and models
566 to expand our understanding of how temperature affects the movement behaviour of other

567 species, including smaller mammals, more elusive species, and non-mammal animals. Un-
568 derstanding of how temperature affects each species in a community will allow us to begin
569 making community-level inferences of how temperature will affect intra-specific interactions
570 from a movement behaviour perspective (Nathan *et al.*, 2008, 2022; Martinez-Garcia *et al.*,
571 2020). While adopting such a perspective is surely not simple, it would result in more com-
572 plete estimates of the effects of climate change on community ecology, particularly when
573 species are exposed to rapid change in many important variables. Future work should ex-
574 plore the effects of temperature on movement behaviour while accounting for finer-scale and
575 species specific variables that were not accounted for in this study. Examples of these include
576 temporally dynamic measures of forest type and age, canopy density, competitive pressures,
577 forage availability, and predator avoidance, or environmental stochasticity. However, many
578 of these data not available, so we also suggest that more work be done on quantifying such
579 measures using spatiotemporally dynamic models and sufficiently fine resolutions.

580 6 Author contributions

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

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