

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

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Alternative titles

- Rising temperatures alter the movement phenology of terrestrial mammals
- Terrestrial mammals alter their movement behavior to rising temperatures

Article type: Research article

Words in abstract: 286

Words in main text: 8239

Figures: 8

Tables: 3

References: 142 (updated on 2025-06-11)

Appendices: 2

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

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 mammalian 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 Introduction

² For most animals, movement is a rapid and low-cost response to a variety of stimuli (Nathan
³ *et al.*, 2008). Animals move to optimize resource use (e.g., food, water, shelter; Charnov,
⁴ 1976; Kacelnik *et al.*, 1992; Merkle *et al.*, 2016; Mezzini *et al.*, 2025), optimize habitat use
⁵ (Schwerdt *et al.*, 2024; Winter *et al.*, 2024), and avoid predators and competitors (Tórrez-
⁶ Herrera *et al.*, 2020; Peterson *et al.*, 2021; Bartashevich *et al.*, 2024; Tan *et al.*, 2024).
⁷ However, ambient temperature affects mammals' movement rates by altering the energetic
⁸ cost of movement (McNab, 1970; Taylor *et al.*, 1982; Brown *et al.*, 2004; Fuller *et al.*, 2016;
⁹ Jahn & Seebacher, 2022) and extreme temperatures can reduce movement rates and cause
¹⁰ physiological damage (Heten *et al.*, 2014; Dyer *et al.*, 2023). Animals may search for a short-
¹¹ term buffer from extreme heat or cold via thermal refugia (Hannah *et al.*, 2014; Elmore *et*
¹² *al.*, 2017; Attias *et al.*, 2018; Arechavala-Lopez *et al.*, 2019; Gulland *et al.*, 2022), which
¹³ may even be preferred over forage abundance (Hall *et al.*, 2016). By altering mammals'
¹⁴ movement speed and habitat use (jointly, their movement behaviour: Nathan *et al.*, 2008,
¹⁵ 2022), ambient temperature also affects the consequences of movement behaviour (Alston
¹⁶ *et al.*, 2020; Giroux *et al.*, 2023), such as encounter rates with resources (Mezzini *et al.*,
¹⁷ 2025), humans (Weststrate *et al.*, 2024), predators, prey, or competitors (Martinez-Garcia
¹⁸ *et al.*, 2020; Glass *et al.*, 2021; Brivio *et al.*, 2024). Behavioural changes to temperature
¹⁹ are exacerbated in extreme cold (Wilson *et al.*, 2001; Berger *et al.*, 2018) and extreme heat
²⁰ (Powers *et al.*, 2017; Alston *et al.*, 2020; Giroux *et al.*, 2023; Verzuh *et al.*, 2023).

²¹ Mammals are particularly susceptible to adverse effects from excessive heat (Sherwood &
²² Huber, 2010). While extreme cold often leads to reduced movement, provided that individ-
²³ uals can find refuge and take advantage of their body heat (Berger *et al.*, 2018; Hou *et al.*,
²⁴ 2020; Glass *et al.*, 2021), extreme heat can often result in more severe physiological damage
²⁵ in a shorter span of time (Jessen, 2001; Sherwood & Huber, 2010; Mota-Rojas *et al.*, 2021;
²⁶ Newediuk *et al.*, 2024). Due to mammals' difficulty at dissipating heat, particularly when am-

bient temperatures are near or above their body temperature, they are particularly sensitive to extreme heat, especially with increasing body size (Dyer *et al.*, 2023; Verzuh *et al.*, 2023). Furthermore, species that experience narrow temperature ranges (i.e., ‘temperature specialists’) tend to be more sensitive to changes (e.g., giant anteaters, *Myrmecophaga tridactyla*: Giroux *et al.*, 2023), while species that experience wide ranges of temperature variation (i.e., ‘temperature generalists’) respond more easily to change (Levins, 1974; Botero *et al.*, 2015; Dupont *et al.*, 2024). Still, generalists’ greater adaptability is tested when they are subject to changes that are more severe (McCain, 2019; Rantanen *et al.*, 2022), affect many factors at once (e.g., temperature, snow depth, ecosystem phenology, and resource availability: Polazzo *et al.*, 2024), or are too rapid and severe to respond to within a lifetime or a few generations (Levins, 1974; Gienapp *et al.*, 2008; Fuller *et al.*, 2016; Xu *et al.*, 2021).

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

54 Cunningham *et al.*, 2021; Melin *et al.*, 2023). However, there remains a need for fine-scale
55 estimates of the effects of temperature on mammals' movement behaviour and quantitative
56 predictions of changes in movement behaviour with climate change in the current century
57 (IPCC, 2023).

58 Western Canada is currently experiencing rapid widespread warming (Turner & Clifton,
59 2009; Kienzle, 2018; Dierauer *et al.*, 2021), phenological shifts (Kienzle, 2018; Basu *et al.*,
60 2024; Tysor, 2025), and more frequent and intense extreme events (Zhang *et al.*, 2023). As
61 we approach the deadline for the Kunming-Montreal Global Biodiversity Framework (i.e.,
62 the "30 by 30" initiative), a global effort to conserve 30% of the world's lands and oceans by
63 2030 (Convention on Biological Diversity, 2022), Canadian decision makers must understand
64 which areas will be of greatest value for maximizing and protecting biodiversity not only for
65 current conditions but future decades, too. Failing to understand how climate change will
66 affect mammalian movement behaviour will hinder our ability to respond to the current
67 climate crisis and make decisions that are viable in the long term. Furthermore, under-
68 standing how temperature affects individual species is the first step towards understanding
69 how temperature impacts the community dynamics (Hegel *et al.*, 2010; Cunningham *et al.*,
70 2021; Carbeck *et al.*, 2022) and habitat phenology (Bunnell *et al.*, 2011; Duncan *et al.*, 2012;
71 Merkle *et al.*, 2016; Slatyer *et al.*, 2022; Gerlich *et al.*, 2025), and how these changes will
72 impact mammals in the coming decades (Sobie *et al.*, 2021; Eum *et al.*, 2023; Weststrate *et*
73 *al.*, 2024).

74 In this paper, we quantify the effects of proximal air temperature on mammalian move-
75 ment behaviour, namely movement rates and habitat selection of six large-bodied terrestrial
76 mammal species in western Canada (boreal and southern mountain caribou: *Rangifer taran-*
77 *dus*, cougars: *Puma concolor*, elk: *Cervus canadensis*, grizzly bears: *Ursus arctos horribilis*,
78 mountain goats: *Oreamnos americanus*, and wolves: *Canis lupus*; Table 1). Using over
79 25 years of telemetry data throughout a large spatial range of western Canada and hourly
80 air temperature data, we estimate how these mammals altered their probability of mov-

81 ing, speed when moving, and habitat selection in response to temperature. We then pair
 82 the estimated responses with climate change projections to forecast the species' movement
 83 behaviour during the 21st century under different climate-change scenarios (referred to as
 84 Shared Socioeconomic Pathways, SSP, Riahi *et al.*, 2017). We discuss the consequences of
 85 these changes in movement behaviour at the individual, population, and community levels.
 86 We also provide directions for future research and solutions for overcoming some common
 87 data limitations.

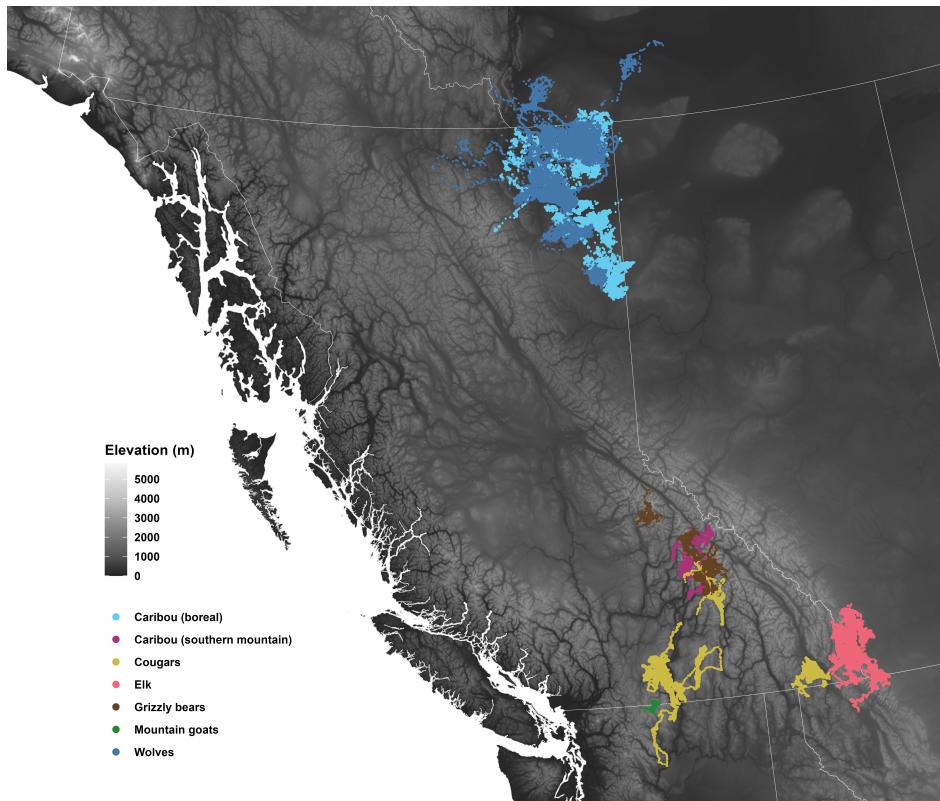


Figure 1: GPS telemetry data for the six species in this study (dots) over a digital elevation model for the study area.

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

Species	Start	End	n	Δt (hours)	Animals	Has speed
Caribou (boreal)	2007-01-13	2013-11-20	875,853	2.00	169	169
Caribou (southern mountain)	2019-06-25	2023-10-05	65,452	6.25	11	10
Cougars	2006-02-05	2021-07-13	80,650	2.00	29	29

Species	Start	End	n	Δt (hours)	Animals	Has speed
Elk	2011-03-02	2018-01-04	200,561	13.00	146	131
Grizzly bears	2004-09-30	2009-09-07	39,021	1.00	18	18
Mountain goats	1998-03-21	2009-06-07	27,921	6.00	22	20
Wolves	2013-01-27	2017-08-29	202,433	0.25	39	39

88 2 Methods

89 2.1 Datasets used

90 This study leverages four main datasets: (1) a multi-species collection of GPS telemetry
 91 data (Fig. 1); (2) historical hourly air temperature from the ERA5 reanalyzed dataset (Euro-
 92 pean Center for Medium-range Weather Forecasting; Hersbach *et al.*, 2023); (3) temporally
 93 static rasters of percent forest cover, elevation, and distance from water; and (4) climate
 94 change projections under four Shared Socioeconomic Pathways (SSPs; Riahi *et al.*, 2017).
 95 While we acknowledge there are other important variables (e.g., forest type, structure, and
 96 age; terrain slope and aspect), we limited our models to only use three simple variables
 97 for the sake of parsimony and comparability across species. See the discussion section for
 98 additional detail on the advantages and limitations of using such simple models.

99 2.1.1 GPS telemetry data

100 Elk data from Ciuti *et al.* (2012) were downloaded from Movebank (Kays *et al.*, 2022). Boreal
 101 caribou and wolf telemtries were acquired from a data repository of the British Columbia
 102 Oil and Gas Research and Innovation Society (BC OGRIS) that was collected as part of the
 103 boreal caribou radio-collaring program of the BC OGRIS Research and Effectiveness Moni-
 104 toring Board (REMB; BC OGRIS, 2018). **MISSING INFO ON OTHER TELEME-**
105 TRY DATA. From the full set of telemetry data, we removed a total of 2396 problematic
 106 GPS locations (0.16%, including collar calibration data) after inspecting diagnostic plots
 107 of (1) distance from the median location, (2) straight-line displacement between locations,

108 (3) turning angle, and (4) time interval between consecutive points. Particular attention
109 was paid to points with large turning angles ($\gtrapprox 170^\circ$) and excessively high straight-line
110 displacement, especially if antecedent and subsequent points indicated relatively stationary
111 behaviour (Appendix A).

112 2.1.2 Historical temperature data and climate change projections

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

119 We used the the `climatenetR` package (v. 1.0, Burnett, 2023) for R and ClimateNA (v.
120 7.4.2; Wang *et al.*, 2016; Mahony *et al.*, 2022) to obtain projected average monthly tempera-
121 tures from 2020 to 2100 at a 0.08° spatial resolution. Since the climate projections only pro-
122 vided monthly means and ranges but no measures of variance or distributional assumptions,
123 we used the historical data for western Canada from 1998 to 2023 (extremes included) to esti-
124 mate the monthly variation in temperature, which we defined as σ_T^2 , the variance at location
125 $\langle x, y \rangle$ in month m for each year (e.g., the variance at coordinates $\langle -119.40, 49.94 \rangle$ in April
126 2005). We then modeled the estimated variance using a Generalized Additive Model (GAM)
127 for Location and Scale (GAMLS, Rigby & Stasinopoulos, 2005; Stasinopoulos & Rigby, 2007;
128 section 7.9 in Wood, 2017) using the `mgcv` package for R (v. 1.9-1, Wood, 2017). The linear
129 predictor for the location (i.e., the mean) included smooth terms of: each year's estimated
130 within-pixel monthly mean temperature ($\hat{\mu}_T$), month (m), a two-dimensional smooth of spa-
131 tial coordinates $\langle x, y \rangle$, and a tensor product interaction term of month and space to allow
132 for seasonal terms to vary smoothly over space. The linear predictor for the scale term,
133 which governs the mean-variance relationship (table 3.1 on p. 104 of Wood, 2017), included

¹³⁴ smooth terms of the monthly mean temperature, month, and space. We did not include
¹³⁵ smooth terms of year to avoid unrealistic projections when extrapolating beyond past 2023.
¹³⁶ The model was thus

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

¹³⁷ where $\mu_{\sigma_T^2}$ and $\nu_{\sigma_T^2}$ indicate the location and scale parameters of the gamma distribution of
¹³⁸ 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
¹³⁹ $f_{S,j}$ indicate the j^{th} smooth functions for the location and scale parameters, respectively.
¹⁴⁰ To ensure the smooth functions of month, $f_{L,2}(m)$ and $f_{S,2}(m)$, joined smoothly between
¹⁴¹ December and January, the terms use cyclic cubic spline bases. The spatial terms used two-
¹⁴² dimensional Duchon splines, a generalization of thin-plate regression splines (p. 221 of Wood
¹⁴³ (2017)). The smoothness parameters were estimated via REstricted Maximum Likelihood
¹⁴⁴ (REML; p. 83 of Wood, 2017). See the Data Availability Statement for additional information
¹⁴⁵ on the code used to fit the model.

¹⁴⁶ We simulated hourly variation in future years by assuming hourly temperature followed
¹⁴⁷ a normal distribution with mean specified by the monthly **climatenaR** climate projections
¹⁴⁸ and variance as specified by the gamma GMLS. For each month within each year from
¹⁴⁹ 2025 to 2100, we simulated hourly weather by including temperatures from the 0.1 to the
¹⁵⁰ 0.9 quantiles by increments of 0.1, and we weighted each quantile proportionally to the
¹⁵¹ (normalized) Gaussian probability density for each quantile.

152 **2.1.3 Resource rasters**

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

166 **2.2 Estimating mammals' instantaneous speeds**

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

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

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

183 **2.3 Estimating the effects of temperature on mammals' movement behaviour**

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

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

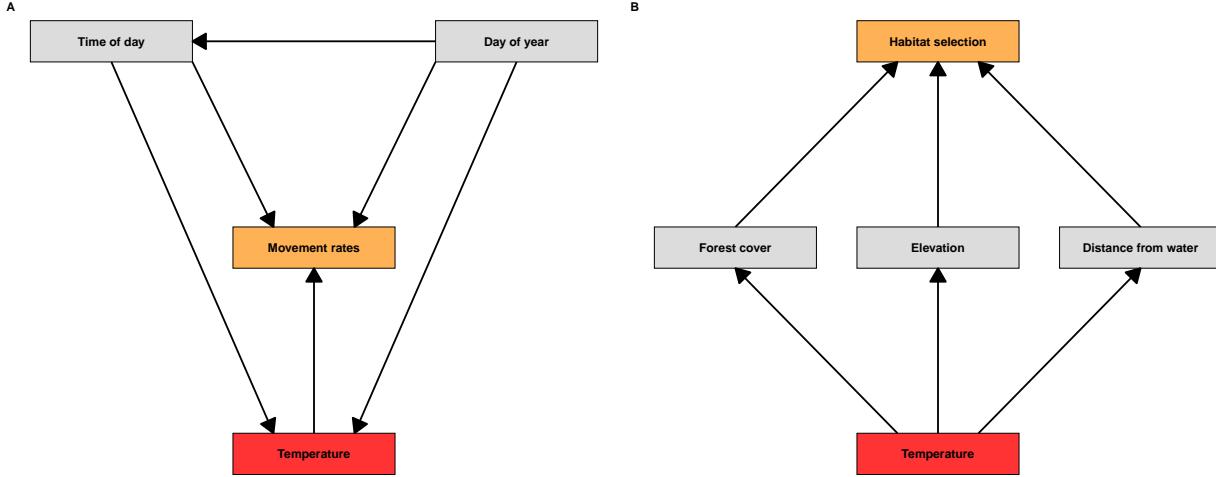


Figure 2: Directed Acyclical Graphs (DAGs) assumed for inferring the causal effects of temperature on each species' movement behaviour. (A) Ambient temperature affects mammals' movement rates (i.e. probability of moving, speed when moving, and distance traveled), but temperature is influenced by time 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.

2.3.1 Effects of temperature on movement rates

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

The HGAMs (equations (2) and (3)) included fixed-effect intercepts for each species (β_s), random intercepts for each animal (Z_a), and species-level `by` smooths that allowed

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

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

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

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

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

238 **2.3.2 Effects of temperature on habitat selection**

239 We estimated the effects of temperature on each species' selection for percent forest cover
240 (`forest_perc`), elevation (`elevation_m`), and distance from water (`dist_water_m`) by fit-
241 ting a Hierarchical Resource Selection Function (HRSF) for each species. We fit each HRSF
242 using an HGAM with a Poisson family of distributions and log link function (Appendix B;
243 Aarts *et al.*, 2008). After removing non-resident individuals (Table B1), we accounted for the
244 spatiotemporal autocorrelation in the telemetry locations by weighting each point based on
245 the telemetry's Autocorrelated Kernel Density Estimate (Fleming & Calabrese, 2017; Noo-
246 nan *et al.*, 2019b; Alston *et al.*, 2022) to produce estimates of second-order habitat selection
247 (Johnson, 1980). Quadrature points were determined using the raster cells in each animal's
248 99.9% AKDE percentile and given a weight of 1. The number of quadrature locations greatly
249 outnumbered the number of observed locations (Fig. B12), especially after accounting for
250 the AKDE weights (Fig. B13).

251 Each species' model had the same structure:

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

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

264 3 Results

265 Of the GPS fixes with finite speed estimates, 2.6% had temperatures lower than -20°C ,
266 while 6.5% had temperatures above 20°C , and temperature ranges differed across species
267 (Table 2, Fig. B2). Sampling interval affected estimates of probability as well of as speed

268 when moving (Fig. B8). Consequently, we present all results while predicting specifically
 269 for one-hour sampling intervals. At 0°C, species differed in mean probabilities of moving
 270 ($\hat{P}(M)$; range: 0.05 – 0.31), mean speed when moving ($\hat{\mathbb{E}}(S|M = 1)$; range: 0.42 – 2.67
 271 km/h), and mean distance traveled (i.e., $\hat{P}(M) \times \hat{\mathbb{E}}(S|M = 1)$, range: 0.04 – 0.61 km/h;
 272 Table 2). Grizzly bears had the lowest movement frequency ($\hat{P}(M) \approx 0.05$), while wolves
 273 and cougars moved most often ($\hat{P}(M) \geq 0.22$). Mountain goats and southern mountain
 274 caribou moved the slowest ($\hat{\mathbb{E}}(S|M = 1) \approx 0.43$ km/h), while wolves had the highest mean
 275 speed when moving ($\hat{\mathbb{E}}(S|M = 1) \approx 2.67$ km/h). Consequently, at 0°C, wolves traveled an
 276 average of 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 GPS fixes with finite speed estimates, namely: the number fixes after data cleaning (n), the percentage of fixes with temperature (T) below -20°C and above 20°C, the estimated mean probability of moving ($\hat{P}(M = 1)$), the mean speed when moving ($\hat{\mathbb{E}}(S)$; km/h), and the 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	n	T < -20°C (%)	T > +20°C (%)	$\hat{P}(M = 1)$	$\hat{P}(M = 1 T)$	$\hat{\mathbb{E}}(S)$	$\hat{\mathbb{E}}(S T)$	$\hat{\mathbb{E}}(D)$	$\hat{\mathbb{E}}(D T)$
Caribou (boreal)	187,679	6.8	7.9	0.05	0.05	0.72	0.72	0.04	0.04
Caribou (s. mountain)	26,518	1.3	3.4	0.15	0.13	0.43	0.42	0.06	0.06
Cougars	80,621	0.7	6.9	0.16	0.17	0.57	0.57	0.09	0.10
Elk	875,682	2.4	4.9	0.11	0.11	0.43	0.42	0.05	0.05
Grizzly bears	39,001	0.0	8.4	0.23	0.22	2.64	2.67	0.61	0.60
Mountain goats	65,219	0.7	2.8	0.27	0.31	0.74	0.76	0.20	0.24
Wolves	202,386	1.7	13.0	0.19	0.18	0.71	0.73	0.14	0.13
Total	1,477,1062.6		6.5						

277 Across all species, Relative Selection Strength (RSS) was weakest for forest cover and
 278 strongest for elevation. At temperatures near 0°C, wolves selected for forest cover ($\gtrapprox 50\%$),
 279 elevations near 1 km, and distances from water < 5 km; elk selected for intermediate forest
 280 cover ($\approx 50\%$), elevations between 1 and 2 km, and distances from water of 10–15 km;
 281 mountain goats selected for sparse forest cover ($< 25\%$), elevations near 1.5 km, and distances
 282 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 $\Delta AIC \geq 342$; 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.

3.1 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 altered 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

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

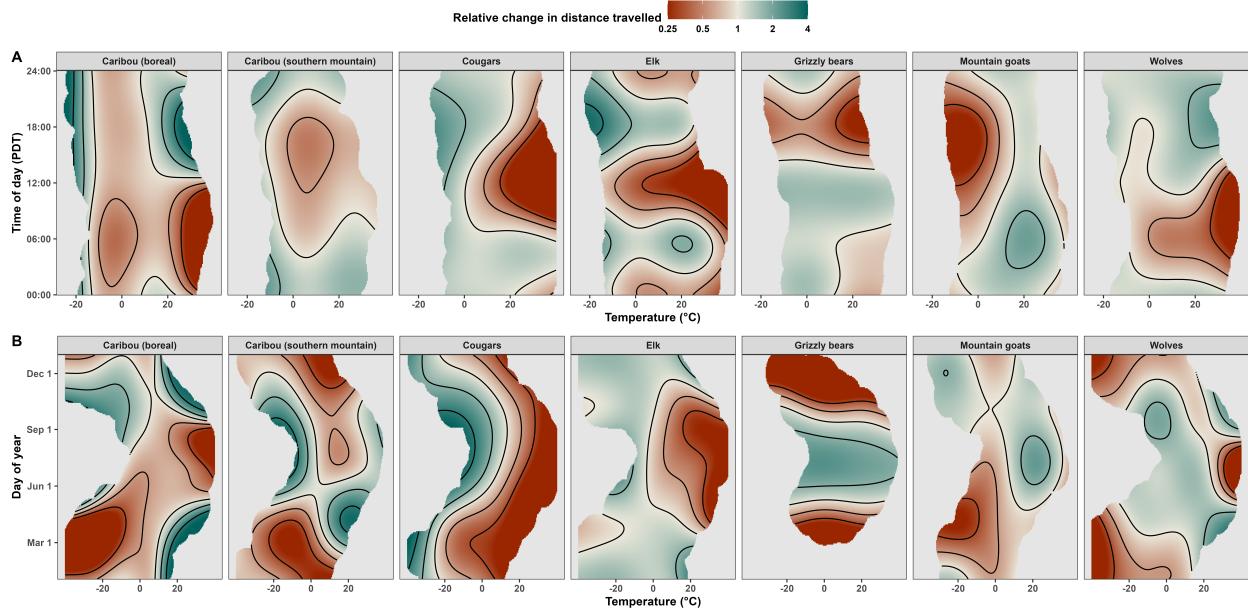


Figure 3: **Temperature is a strong determinant of how far and when mammals travel.** The fill indicates the effects of temperature on the relative change in distance travelled (probability of moving times mean speed when moving) over time of day on June 1st (A) and day of year at 12:00 PDT (B). Predictions in the surface plots extend to 10% of the range away from each datum. The color bar is on the \log_2 scale to help visualize patterns in doubling, and values are capped to $2^{\pm 2}$ for ease of readability.

312 3.2 Effects of temperature on habitat selection

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

322 50% forest cover or less. All species shifted elevationally with temperature, although boreal
 323 caribou had a much sharper change in RSS across elevation. Elk, mountain goats, and cougars
 324 moved to higher elevations with temperature, while wolves, southern mountain caribou, and
 325 grizzly bears moved to lower elevations. Wolves, elk, and southern mountain caribou moved
 326 closer to water with temperature, while mountain goats, cougars, and grizzly bears moved
 327 somewhat further away from water but remained mainly within 5-10 km of water. As with
 328 movement rates, estimated RSS was generally most uncertain at extreme temperatures, for
 329 which data was scarcer (Fig. B15).

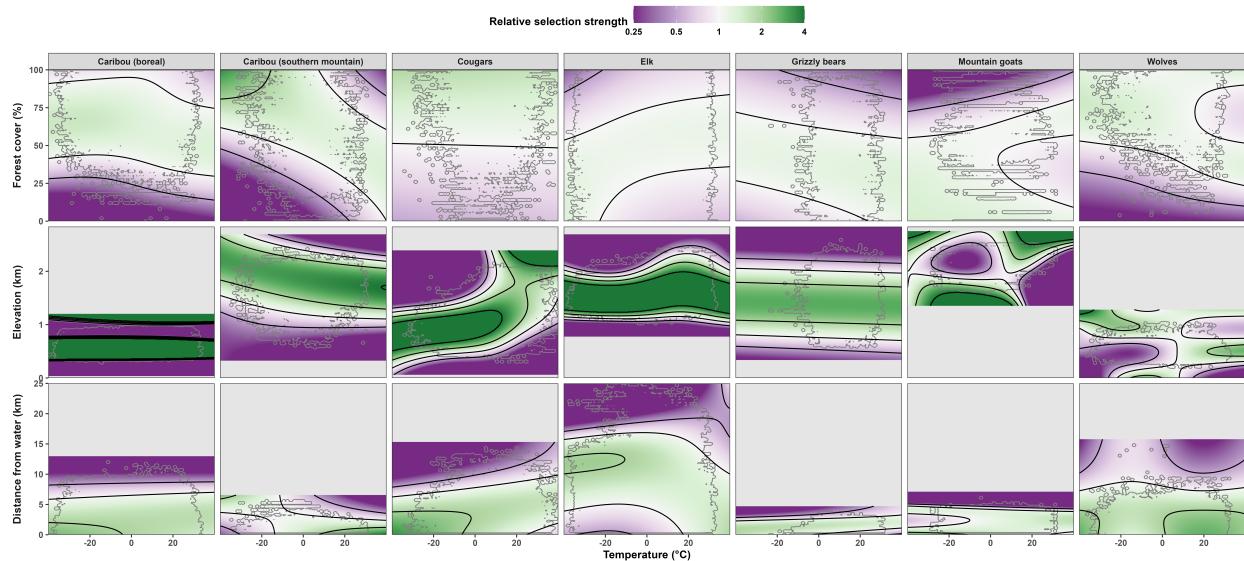


Figure 4: Mammals' habitat selection depends on ambient temperature. Estimated relative selection strength (RSS) for forest cover (%), elevation (km), and distance from water (km) as a function of temperature. The grey contours indicate the extent of each species' observed data. RSS values were re-centered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

330 3.3 Predicted changes in movement behaviour during the 21st century

331 Predicted changes in movement rates with future climate change varied across species in both
 332 magnitude and direction, but worse SSPs always corresponded to greater absolute changes
 333 (Fig. 5). Additionally, species that were predicted to move less often did not necessarily have
 334 lower speeds when moving, and vice versa (Figs. B9 and B10). Absolute relative changes in
 335 average yearly distance travelled were small under the best-case SSP (0-4% change in 2100
 336 relative to 2025). Under the worst-case SSP, absolute changes by 2100 (relative to 2025)

337 ranged from ~2% (grizzly bears) to ~24% (cougars). Notably, while the models estimated
 338 that grizzly bears would move substantially less (if at all) in late fall and winter (Figs. 3, B4),
 339 the models did not explicitly account for changes in hibernation phenology. Consequently,
 340 the climate change projections do not explicitly account for changes in energetic needs or
 341 physiology. Projected changes in 2100 varied spatially due to spatial heterogeneity in climate
 342 change projections (Fig. 6). Again, absolute changes were generally greatest under worse
 343 SSPs, but the direction of change at each location also varied across SSPs (most visible in
 344 cougars).

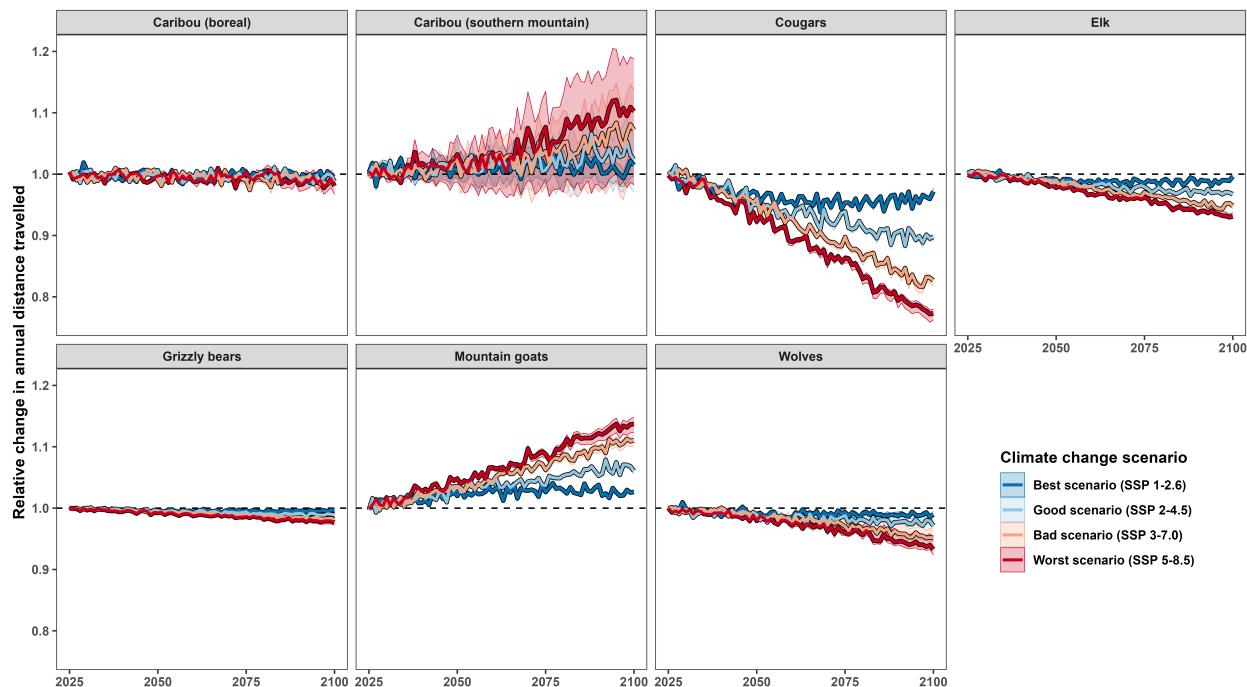


Figure 5: Species will alter their movement rates differently in response to climate change, but worse climate-change scenarios will result in the greatest change. Bold lines indicate the median change in distance travelled (probability of moving times speed when moving) due to predicted changes in temperature 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.

345 Median RSS was projected to decrease over time within the each species' observed range,
 346 but, again, changes were stronger under worse SSPs (Fig. 7). Decreases were most pro-
 347 nounced in areas with the lowest RSS and most severe for elk, mountain goats, pumas, and
 348 southern mountain caribou. Changes for boreal wolves and caribou were relatively negli-

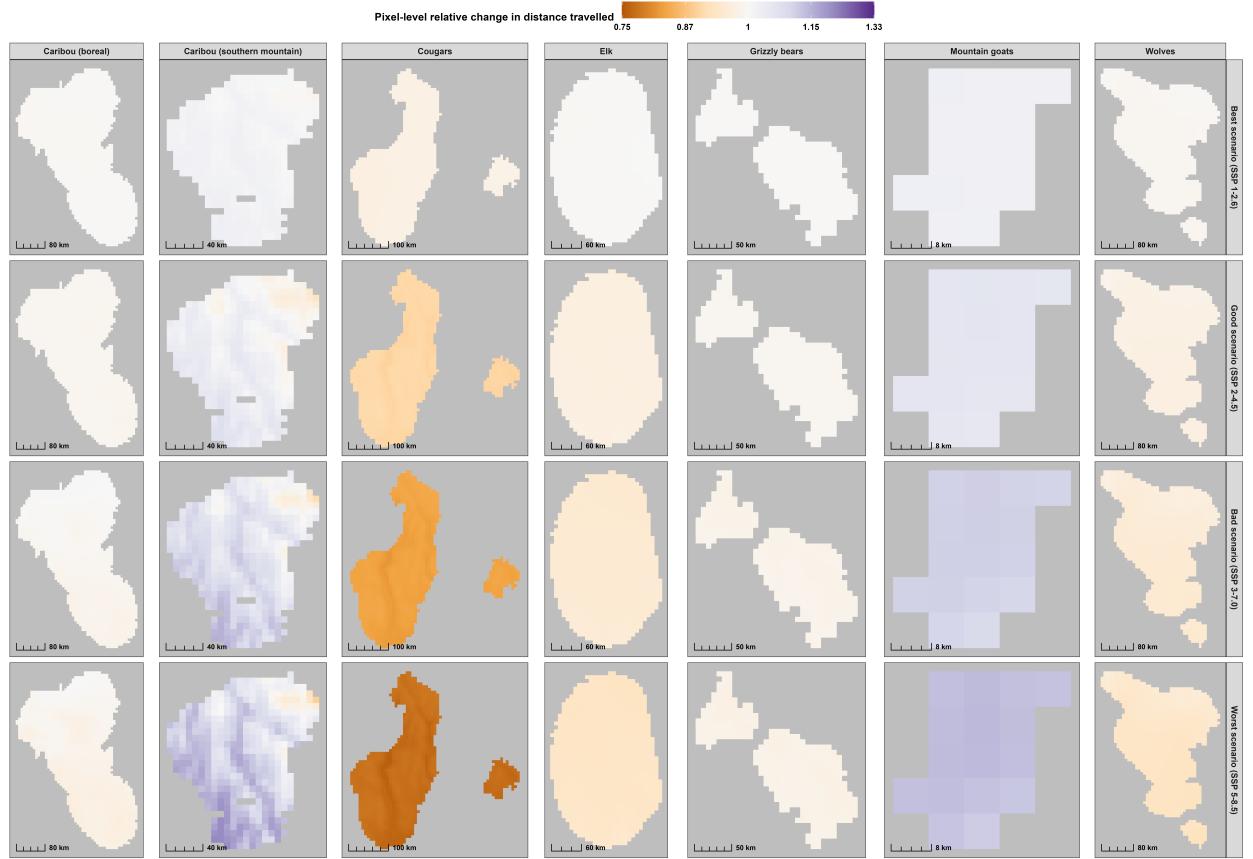


Figure 6: Climate change will impact each species' movement rates differently, but changes will also vary spatially. The color of each pixel indicates the predicted changes in distance traveled in 2100 at that pixel, relative to the value in 2025, averaged across all four scenarios. Values < 1 indicate 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).

349 gible. Elk, cougars, and grizzly bears were predicted to increase their selection strength
 350 for top-RSS areas, and elk, mountain goats, cougars, and southern mountain caribou were
 351 predicted to further decrease their selection for areas with low RSS. Unsurprisingly, the
 352 change in RSS between 2025 and 2100 also varied spatially for all species (Fig. 8). Overall,
 353 RSS decreased throughout most of each species' current range, although elk, cougars, and
 354 bears were predicted to increase their selection for higher-altitude habitats. Still, none of
 355 the species were projected to increase RSS throughout their habitat (9).

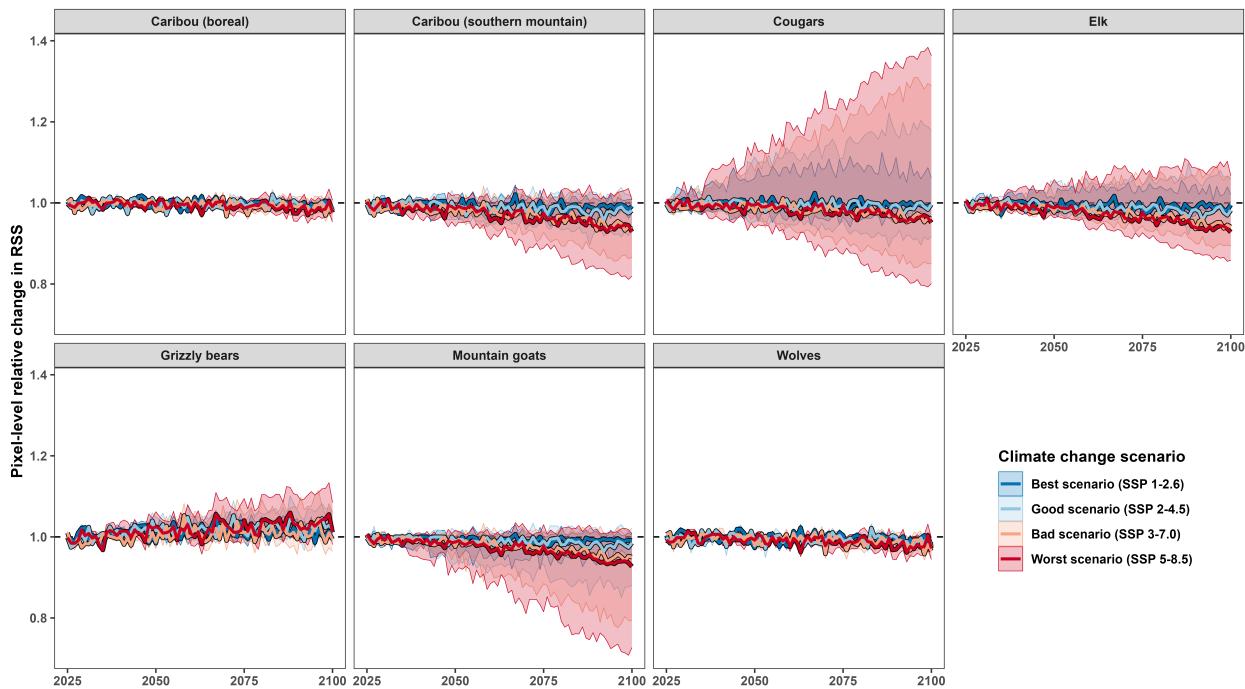


Figure 7: Species will alter their habitat selection differently in response to climate change, but worse climate-change scenarios will result in the greatest change. Bold lines indicate the change in median RSS due to predicted changes in temperature within each species' observed extent. Shaded areas 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).

356 4 Discussion

357 We have demonstrated that temperature is an important determinant of how and where
 358 large mammals move, and that mammals alter their seasonal and daily cycles in movement
 359 behavior in response to changes in temperature. Predicting mammals' responses to climate



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).

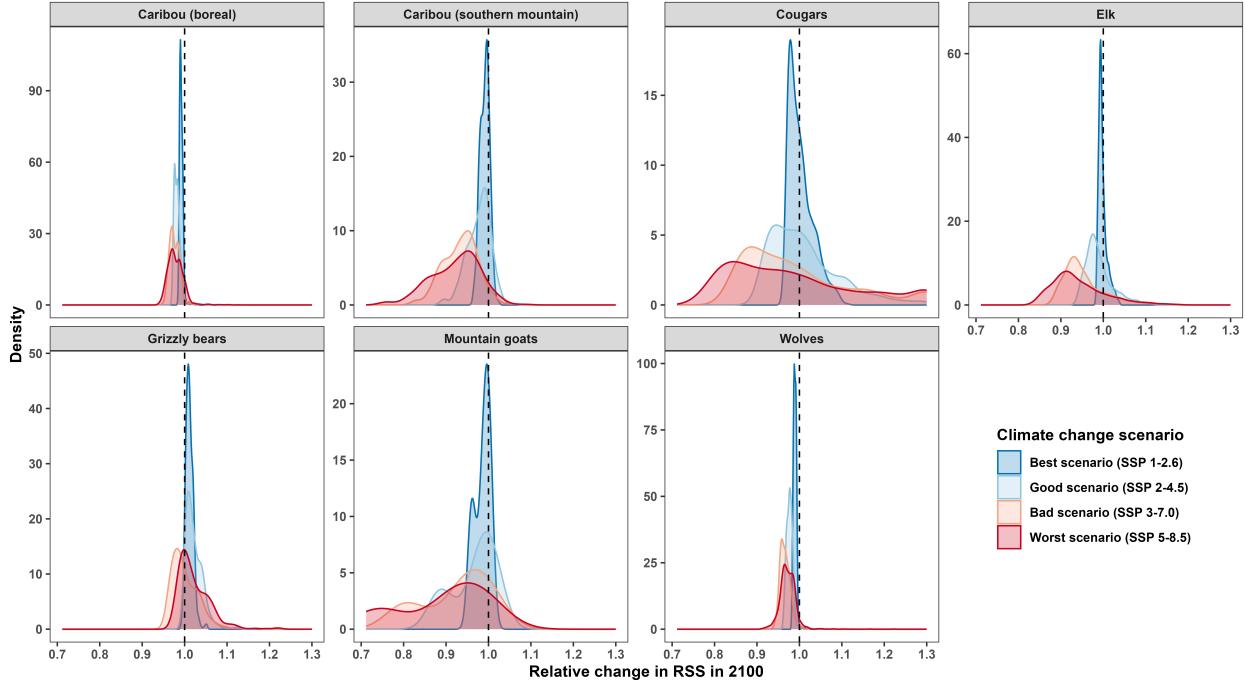


Figure 9: Climate change will cause species to decrease their selection strength for their current habitats, but worse climate change scenarios will have the greatest impact. The density plots indicate each species’ change in RSS in 2100 for their current habitat (Fig. 8), relative to each location’s 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).

change remains a challenge, as habitats warm rapidly and mammals are exposed to increasingly novel and extreme conditions (Diffenbaugh & Field, 2013; Botero *et al.*, 2015; IPCC, 2023). We leveraged the flexibility and interpretability of GAMs to estimate the (nonlinear) responses of terrestrial mammals to temperature. In particular, tensor product interaction terms were crucial for estimating smooth, nonlinear changes in daily and seasonal trends with temperature. By allowing interaction terms to be smooth bivariate functions, we were able to quantify changes in movement behavior without the need to discretize time into distinct windows (e.g., day/night and seasons). We were thus able to present changes using relatively simple and interpretable surface plots (Figs. 3 and 4) that conveyed detailed and nuanced estimates of change. This framework was essential for estimating how mammals behave in extreme conditions for which data are scarce.

As temperatures warm, mammals’ risk of hyperthermia increases nonlinearly (Sherwood & Huber, 2010), especially for large-bodied species (Alston *et al.*, 2020; Dyer *et al.*, 2023;

³⁷³ Verzuh *et al.*, 2023). The recent increase in frequency and duration of extreme-temperature
³⁷⁴ events (Bunnell *et al.*, 2011; Kienzle, 2018; Yao *et al.*, 2022; IPCC, 2023; Zhang *et al.*, 2023)
³⁷⁵ have forced many mammals towards increasingly atypical behaviours with long-term conse-
³⁷⁶ quences, ranging from changes in the behavior and fitness of individuals (Cunningham *et al.*,
³⁷⁷ 2021; Brivio *et al.*, 2024) to mass die-offs (Ameca y Juárez *et al.*, 2012). A species' ability
³⁷⁸ to respond to changing temperature and phenology depends mainly on the its exposure,
³⁷⁹ sensitivity, and adaptability to changes, and growing evidence suggests that many mammals
³⁸⁰ in western Canada will struggle to respond due limitations in all three factors (Ameca y
³⁸¹ Juárez *et al.*, 2012; Diffenbaugh & Field, 2013). Firstly, exposure to warming temperatures
³⁸² is widespread throughout the area, and warming is expected to accelerate over the coming
³⁸³ decades (Bunnell *et al.*, 2011; Diffenbaugh & Field, 2013; Kienzle, 2018; Eum *et al.*, 2023;
³⁸⁴ IPCC, 2023). Secondly, large-bodied mammals are particularly sensitive to high heat (Dyer
³⁸⁵ *et al.*, 2023), but small-bodied mammals are also affected (Krebs *et al.*, 2019; Ratnayake
³⁸⁶ *et al.*, 2019). Finally, species' adaptability is tested by the speed of climate change (Diff-
³⁸⁷ enbaugh & Field, 2013) and the rigidity of many speices' photoperiod-dependent phenology
³⁸⁸ (Walker *et al.*, 2019).

³⁸⁹ Our results suggest that climate change will cause mammals to alter their seasonal move-
³⁹⁰ ment behavior, but not all species will respond similarly. For example, hotter temperatures
³⁹¹ caused boreal caribou to travel longer distances in fall, winter, and spring but less in sum-
³⁹² mer, mirroring the findings of Stien *et al.* (2012), Leclerc *et al.* (2021), and Lessard *et*
³⁹³ *al.* (2025). The increase in movement rates during the colder seasons are likely partly due
³⁹⁴ to shallower snow depth that results in greater mobility (Pedersen *et al.*, 2021), but rising
³⁹⁵ temperatures during snowy seasons also increase the chances of rain-on-snow events, which
³⁹⁶ limit forage availability and increase the ungulates' need to search for food (Stien *et al.*,
³⁹⁷ 2012; Berger *et al.*, 2018; Mezzini *et al.*, 2025). In contrast, the reduced movement rates
³⁹⁸ during warmer summers are likely mainly due to caribou searching for shelter from the heat
³⁹⁹ due to ungulates' elevated risk of hyperthermia (Alston *et al.*, 2020; Verzuh *et al.*, 2023).

400 The effects of extreme temperatures are exacerbated by phenological mismatches with sea-
401 sonal photoperiod (Walker *et al.*, 2019), including the timing of molting and reproduction.
402 Earlier growth seasons in boreal and arctic regions have resulted in lower calf birth and sur-
403 vival (Post & Forchhammer, 2008), while the lengthening of the growth season has allowed
404 moose (*Alces alces*) and deer (*Odocoileus* spp.) to encroach on boreal caribou habitat, along
405 with increased density of coyotes (*Canis latrans*), cougars, and wolves (Barber *et al.*, 2018;
406 DeMars *et al.*, 2023). Thus, rising temperatures affect more than each individual species'
407 movement behavior; they have complex and interconnected effects on an entire community
408 and its trophic structure.

409 Our results suggest that rising temperatures will have similar effects on boreal wolves.
410 Warmer temperatures caused wolves to travel further throughout the year, but, similarly
411 to boreal caribou, they moved substantially less at temperatures above 25°C in summer.
412 At temperatures above 20°, both boreal caribou and wolves tended to move less during the
413 day and more between 17:00 and 24:00. This synchronicity in movement patterns is likely
414 to increase encounters between the two species, particularly when coupled with increasing
415 human disturbances, since wolves leverage seismic lines and other anthropogenic linear fea-
416 tures (e.g., roads) to reduce movement costs while increasing the chances of encountering
417 prey (Whittington *et al.*, 2011; Dickie *et al.*, 2017; Dickie *et al.*, 2022). Additionally, caribou
418 that attempt to reduce predation risk from wolves by avoiding wolf habitat may risk increas-
419 ing predation pressure from bears (Leblond *et al.*, 2016) and other encroaching predators
420 (DeMars *et al.*, 2023). As temperatures rise and allow new competitors and predators to
421 encroach on boreal caribou habitat (Barber *et al.*, 2018; DeMars *et al.*, 2023; Labadie *et al.*,
422 2023), climate change will have complex consequences not only for individual species but for
423 entire communities and their trophic interactions.

424 Considerations about changes in trophic interactions leads to an important caveat about
425 the results we present. The estimated effects of temperature on movement behavior cannot
426 be fully attributed to physiological responses to changes in temperature alone, since other

427 aspects of habitats' seasonal phenology are (nonlinearly) correlated with temperature. For
428 example, mountain goats' reduced movement rates at temperatures near 0°C in winter may
429 be due to increased movement difficulty, since melting snow and rain-on-snow events affect
430 the energetic costs of movement (White, 2025) and encounter rates with predators (Sullender
431 *et al.*, 2023). However, milder temperatures can also increase plant growth, which, in turn,
432 allows goats to spend less time searching for forage (White *et al.*, 2025). Therefore, the
433 figure 3 illustrates an estimate of the total effect of temperature on each species movement
434 rates, but it does not explicitly account for energetic costs. Similarly, species' changes in
435 habitat selection do not explicitly account for any changes in physiological or energetic costs.
436 Both mountain goats and elk selected for higher elevation as temperatures warmed, but our
437 models did not explicitly account for differences in forage availability at different altitudes.

438 Forage quality and availability is often a limiting factor for mammals' ability to adapt
439 to warming temperatures by moving to higher altitudes. Plants are slower to arrive in and
440 establish in new habitats than mammals, and the advance of herbivores can further limit
441 plants' ability to establish (Speed *et al.*, 2012; Diffenbaugh & Field, 2013). Consequently,
442 mammals that move to higher elevations may be forced to spend more time foraging (Mezzini
443 *et al.*, 2025), which will increase their energetic expenditure as well as their chances of en-
444 countering predators (including cougars and grizzly bears) or competitors (Kohl *et al.*, 2019;
445 Martinez-Garcia *et al.*, 2020; Tórrez-Herrera *et al.*, 2020; Smith *et al.*, 2023). Additionally,
446 plants at high elevations may be have weaker defenses against herbivory and be more suscep-
447 tible to overgrazing (Callis-Duehl *et al.*, 2017). The scarcity and susceptibility of forage may
448 thus limit herbivores' ability to shift elevationally, particularly if predation rates remain
449 relatively unchanged or increase. Furthermore, the physical upper limit to elevation can
450 cause individuals to become trapped . If local peaks become unsuitable habitat, and moving
451 to nearby higher peaks requires traveling across low-quality and high-risk habitat (Figure
452 8), habitat fragmentation may become too excessive to move across patches or alternative
453 ranges (White *et al.*, 2025). Translocating animals to locations with higher peaks may help

454 avoid such a scenario, but the success of relocations can be highly species-dependent, and
455 attempts are not always successful (Ranc *et al.*, 2022; White *et al.*, 2025).

456 Changes in mammals' seasonal movement behavior are also likely to affect the timing
457 and frequency of human-wildlife interactions. Since heat affects mammals' sleep quality and
458 likelihood to enter torpor (Fjelldal *et al.*, 2021; Wells *et al.*, 2022; Mortlock *et al.*, 2024),
459 future decades may see increased levels of incidents with bears that struggle to enter or
460 remain in hibernation (Johnson *et al.*, 2018). The risk is further increased when bears' are
461 unable to meet their increased energetic requirements through foraging or hunting. Projected
462 increases in park attendance due to rising temperatures and human population density in
463 Western Canada are expected to further increase frequency of human-wildlife interactions
464 (Weststrate *et al.*, 2024).

465 4.1 Consequences for conservation

466 Species' adaptability to rising temperatures is challenged by the aforementioned simulta-
467 neous, multifarious, and interconnected stressors caused by climate change, since responding
468 to many concurrent changes at once is particularly difficult (Diffenbaugh & Field, 2013;
469 Polazzo *et al.*, 2024). Locations may thus not be able to support species and population
470 sizes they supported historically, and species may thus not select for historical geographical
471 ranges in the future. It is therefore crucial for conservationists and other decision-makers
472 to distinguish between a species' ideal environmental space (or E space, *sensu* Matthiopoulos,
473 2022), and its best available geographic space (or G space, *sensu* Matthiopoulos, 2022).
474 Accelerating multifarious change in species' movement behavior and energetic costs require
475 conservation measures to be proactive and anticipate future changes, even when future con-
476 ditions are substantially different from historical conditions and historical data may not be
477 available. To this end, the framework presented by Polazzo *et al.* (2024) for estimating
478 species' responses to multifarious change becomes essential, particularly when accounting
479 for energetic and fitness costs, as argued by Cunningham *et al.* (2021).

480 As of December 2024, only 13.8% of terrestrial Canada was within protected areas or
481 other conserved areas (Environment and Climate Change Canada, 2025), so rapid action
482 is necessary to protect additional 16.2% of Canada's land by 2030 in accordance with
483 Kunming-Montreal Global Biodiversity Framework (i.e., the “30 by 30 initiative”; Conven-
484 tion on Biological Diversity, 2022). However, the choice of what habitats to protect will re-
485 quire careful consideration, since protected areas should support species not only in present
486 conditions but also as species' needs and selection change over the coming decades (Simmons
487 *et al.*, 2021). As anthropogenic activity increasingly alters habitats and community struc-
488 tures (Sih *et al.*, 2011; Tucker *et al.*, 2018; Rice, 2022; Rosenthal *et al.*, 2022), protecting
489 biodiversity and the habitats it depends on will require widespread and collaboration with
490 local stakeholders, especially Indigenous Peoples, to ensure that all decisions are culturally
491 sound and respect Treaties (Turner & Clifton, 2009; Desjardins *et al.*, 2020; Wong *et al.*,
492 2020; Hessami *et al.*, 2021; Falardeau *et al.*, 2022; Lamb *et al.*, 2023). Understanding the
493 consequences of climate change in mammalian movement behaviour is a first step towards
494 proactively responding to how mammals will respond to human-induced rapid environmental
495 change (Sih *et al.*, 2011; Williams & Blois, 2018). However, a better understanding of such
496 consequences will require a more holistic approach that includes carefully data collection,
497 model design, and interpretation and application of results.

498 **4.2 Study limitations and considerations for future work**

499 ***HERE***

500 Estimated selection strength for forest cover was weak and did not change strongly with
501 temperature. Time-varying rasters of forest cover would have likely given stronger (and
502 better) estimates.

- 503 • variation among individuals: Jeltsch *et al.* (2025). Population-level means that ignore
504 such variation can greatly limit the efficacy of conservation projects (Muff *et al.*, 2020;
505 Mortlock *et al.*, 2024; Silva *et al.*, 2025).

- 506 • we see clear signals despite the data issues and limitations, but more work needs to be
507 done to disentangle important drivers

508 More work is necessary on quantifying interspecific responses to temperature, including
509 the effects of temperature on predation rates (but see: Cunningham *et al.*, 2021; Glass *et*
510 *al.*, 2021; Brivio *et al.*, 2024). The increase in intensity and frequency of extreme heat events
511 (Bunnell *et al.*, 2011; Yao *et al.*, 2022) will likely also impact the occurrence and timing of
512 hibernation (Wells *et al.*, 2022) and migration or seasonal range expansions (Morley, 2021;
513 Carbeck *et al.*, 2022; Malpeli, 2022). However, not all species may be able to adapt at
514 the current rate of climate change (Heten *et al.*, 2014; Williams & Blois, 2018), especially
515 since landscape changes will likely depend not only on the direct effect of temperature but
516 also on cascading changes in the availability and unpredictability of resources (McLellan &
517 McLellan, 2015; Pigeon *et al.*, 2016; Mezzini *et al.*, 2025).

518 Future work should explore the effects of temperature on movement behaviour while
519 accounting for finer-scale and species specific variables that were not accounted for in this
520 study. Examples of these include temporally dynamic measures of forest type and age, canopy
521 density, competitive pressures, forage availability, and predator avoidance, or environmental
522 stochasticity. However, many of these data not available, so we also suggest that more
523 work be done on quantifying such measures using spatiotemporally dynamic models and
524 sufficiently fine resolutions. ... animals in the study are generalists; we need more work on
525 specialists and smaller species, but they can be harder to track

526 changes in the phenology of plants, fire, ice, or mammalian physiology (e.g., moulting,
527 fat storage) or behaviour (e.g., migration, food caching), other than as direct responses to
528 temperature.

- 529 • other confounding causes of movement (forest age, structure, fire, type, dist_water,
530 etc.) change over the years but are assumed to be fixed
- 531 • the temporal resolution of climate change projections isn't great (many steps necessary

532 to simulate weather)

533 ***old text:***

534 Our work highlights three central considerations for future research:

535 (1) tree cover data should vary over time to account for changes over time due to fires and
536 logging

537 (2) telemetry fixes should be frequent enough to reconstruct animals' movement paths and
538 estimate speed (Noonan *et al.*, 2019a; Nathan *et al.*, 2022; Pease, 2024),

539 (3) the number of individuals tracked and the duration of each telemetry should depend
540 not just on population size but also the (accelerating) rate of environmental change,
541 and

542 (4) predicting changes in movement behaviour becomes highly complex when responses
543 are nonlinear, especially when changes depend on many interacting factors (Polazzo *et*
544 *al.*, 2024) and one is interested in predicting responses in extreme conditions for which
545 data are scarce (Steixner-Kumar & Gläscher, 2020).

546 While the `ctmm` movement models produced scale-independent estimates of speed (i.e.,
547 model interpretation is independent of sampling interval: Noonan *et al.*, 2019a), the accu-
548 racy, size, and stability of speed estimates still depended on the GPS sampling frequency.
549 This dependency is because coarsely-sampled movement data contains information on large-
550 scale movements (range crossings, migrations) but not fine-scale movements (Noonan *et al.*,
551 2019a; Nathan *et al.*, 2022), including first-order habitat selection (Johnson, 1980). Using
552 the boreal caribou as an example, the 13-hour sampling interval allows us to reasonably
553 estimate the caribou's movement path at a temporal scale of approximately 13 hours (or
554 greater), but we cannot produce reasonable movement trajectories at a much finer (e.g.,
555 hourly) scale. Consequently, we suggest being cautious when comparing estimated move-
556 ment behaviours across species, even though all predictions have been corrected to the hourly

timescale by predicting for 1-hour time intervals. Ideally, sampling schedules should be fine enough to reconstruct individuals' movement paths. *make data useful for future studies. recognize cost of GPS and suggest IoT (Wild et al., 2023), although station coverage can be a limitation (denicola_monitoring_2025?).* Good estimates of an animal's speed and trajectory require telemetry locations to be taken more often than the animal's directional persistence (Noonan *et al.*, 2019a), so that, on average, the dataset contains multiple locations in between changes in direction. What constitutes a change in direction depends on what movement scale one is investigating. Small-scale movements and first-order spatial selection will require more frequent sampling than migratory movement or second-order and third-order spatial selection. While ctmm movement models are scale-invariant in that any model can be scaled to larger or smaller areas and timescales (Noonan *et al.*, 2019a), the model estimates are not independent of the scale of the sampling frequency (DeNicola *et al.*, 2025). When tracking data are too coarse for accurate speed estimation, diffusion rates (measured in area per unit time) may be a useful alternative for quantifying animals' exploration rates (DeNicola *et al.*, 2025). *also need better way to distinguish between sates. HMMs are an option, but there are limitations.*

573 Other refs and miscellaneous maerial

574 GAMs' flexibility and complexity can also be a frustrating limitation if used too generously. As such, analysts should chose the basis size for each smooth term carefully. While 575 penalized splines and REML can help avoid unruly smooth terms that would result in questionable 576 estimates where data are scarce (Wood, 2017), it is best to select the basis size 577 of the smooth terms with parsimony, especially when datasets are large. Still, predicting 578 mammals' responses at the data-scarce fringes of the surface plots in Figs. 3 and 4 comes 579 with greater uncertainty, particularly given that the changes are nonlinear. 580

581 **Author contributions**

582 SM performed the data cleaning, ran the analyses, and wrote the manuscript. CHF wrote
583 code for estimating instantaneous movement speeds. MJN conceived of the project idea and
584 supervised SM throughout the project. All other authors, which are listed in alphabetical
585 order by last name, contributed telemetry data and reviewed the interpretation of the results
586 for their species of interest. All authors contributed to reviewing the manuscript. **TO FIX**
587 ***BASED ON COMMENTS FROM OTHER AUTHORS DURING REVIEW***

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