

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 few disentangled them from seasonal behaviour cycles. Consequently, it is still uncertain how mammals will adapt their movement behaviour throughout the 21st century. We address this gap by quantifying 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 significantly affects of how and where these mammals move, and we predict that climate change will have significant impacts on mammals' movement behaviour throughout the 21st century. Notably, we found that species did not respond uniformly to temperature. This suggests that community-level responses will be complex, as future climate change drives some species to move more and others less. Median habitat selection strength was predicted to decrease for most species, but some species are expected to show increased selection strength for higher altitudes. Consequently, our results suggest that individuals from all six species may shift their range in the coming decades as they begin to select against portions of their current ranges. The strong but varied responses to temperature suggest that future climate change will impact not only individuals' movement behaviour but also entire communities, as changes in movement behaviour will affect encounter rates, including predator-prey dynamics and human-wildlife interactions. As climate change exposes mammals to novel environmental conditions, proactively anticipating changes in mammalian movement behaviour will become crucial for effectively and proactively understanding community-level responses and selecting high-quality habitat for long-term conservation.

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 (Winter *et al.*, 2024), and avoid predators and competitors (Tórrez-Herrera *et al.*, 2020; Pe-
⁶ terson *et al.*, 2021; Bartashevich *et al.*, 2024; Tan *et al.*, 2024). How and where animals move
⁷ thus determines encounter rates with resources (Mezzini *et al.*, 2025), humans (Weststrate
⁸ *et al.*, 2024), predators, prey, and competitors (Martinez-Garcia *et al.*, 2020; Glass *et al.*,
⁹ 2021; Brivio *et al.*, 2024). However, ambient temperature affects animals' movement rates
¹⁰ by altering the energetic cost of movement and thermoregulation (McNab, 1970; Taylor *et*
¹¹ *al.*, 1982; Brown *et al.*, 2004; Fuller *et al.*, 2016; Jahn & Seebacher, 2022), and extreme
¹² temperatures can reduce movement rates (Dyer *et al.*, 2023) and even cause physiological
¹³ damage and death (Heten *et al.*, 2014; Ratnayake *et al.*, 2019; Schmidt *et al.*, 2020). An-
¹⁴ imals may search for a short-term buffer from extreme heat or cold by moving to thermal
¹⁵ refugia (Hannah *et al.*, 2014; Elmore *et al.*, 2017; Attias *et al.*, 2018; Arechavala-Lopez *et al.*,
¹⁶ 2019; Gulland *et al.*, 2022), and shelter may even be preferred over forage abundance (Hall
¹⁷ *et al.*, 2016). Changes in climate throughout the 21st century and the simultaneous increase
¹⁸ in frequency and intensity of extreme-heat events (Bunnell *et al.*, 2011; IPCC, 2023) are
¹⁹ expected to impact not only animals' movement behavior but also their physiology (Pow-
²⁰ ers *et al.*, 2017; Schwerdt *et al.*, 2024), life history (Newediuk *et al.*, 2024), and phenology
²¹ (Johnson *et al.*, 2018; Carbeck *et al.*, 2022).

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

27 2021; Newediuk *et al.*, 2024). Due to mammals' difficulty at dissipating heat, particularly
28 when ambient temperatures are near or above their body temperature, they are particularly
29 sensitive to extreme heat, especially with increasing body size. Large-bodied mammals are
30 most likely to show changes in movement behaviour with rising temperatures, since they
31 tend to move long distances (Merkle *et al.*, 2016), are particularly sensitive to overheating
32 (Fuller *et al.*, 2016; Verzuh *et al.*, 2023), and their movement rates are thus strongly limited
33 by excessive heat (Dyer *et al.*, 2023).

34 In the last century, many ecosystems experienced widespread warming that resulted in
35 milder and shorter winters, hotter and longer summers, and a greater risk of extremely high
36 temperatures (IPCC, 2023). As heat stress intensifies over the next 100 years, mammals will
37 continue to suffer impacts on their fitness, movement rates, and habitat selection (Deb *et*
38 *al.*, 2020; Woo-Durand *et al.*, 2020), which will be exacerbated by more frequent and intense
39 extreme events (Bunnell *et al.*, 2011) and anthropogenic habitat loss, modification, and frag-
40 mentation (Sawyer *et al.*, 2009; Sih *et al.*, 2011; Weststrate *et al.*, 2024). It remains unclear
41 how or whether species will be able to respond to climate change in the current century
42 (Deb *et al.*, 2020; Woo-Durand *et al.*, 2020; Verzuh *et al.*, 2023), especially if populations
43 fail to adapt to changes (Botero *et al.*, 2015; Sawyer *et al.*, 2019) or are physiologically
44 incapable to do so (Sherwood & Huber, 2010; Williams & Blois, 2018). Preparing for and
45 responding to future changes will require a detailed understanding of how temperature will
46 affect how and where different mammalian species move (Cunningham *et al.*, 2021). Re-
47 cent work has documented the effects of climate change on mammals' ranges (Leclerc *et al.*,
48 2021), thermoregulation (Mota-Rojas *et al.*, 2021), and movement behaviour (McCain, 2019;
49 Cunningham *et al.*, 2021; Melin *et al.*, 2023). However, there remains a need for fine-scale
50 estimates of the effects of temperature on mammals' movement behaviour and quantitative
51 predictions of changes in movement behaviour with climate change in the current century
52 (IPCC, 2023).

53 **CLEAN UP PARAGRAPH BELOW**

54 In this paper, we quantify the effects of proximal air temperature on mammalian move-
 55 ment behaviour, namely movement rates and habitat selection of six large-bodied terrestrial
 56 mammal species in western Canada (boreal and southern mountain caribou: *Rangifer taran-*
 57 *dus*, cougars: *Puma concolor*, elk: *Cervus canadensis*, grizzly bears: *Ursus arctos horribilis*,
 58 mountain goats: *Oreamnos americanus*, and wolves: *Canis lupus*; Table 1). Western Canada
 59 is currently experiencing accelerating and widespread but spatially heterogeneous warming
 60 (Turner & Clifton, 2009; Kienzle, 2018; Dierauer *et al.*, 2021), phenological shifts (Kienzle,
 61 2018; Basu *et al.*, 2024; Tysor, 2025), and more frequent and intense extreme heat events
 62 (Zhang *et al.*, 2023). Canadian decision makers must understand which areas will be of
 63 greatest value for maximizing and protecting biodiversity not only for current conditions but
 64 future decades, too. Failing to understand how climate change will affect mammalian move-
 65 ment behaviour will hinder our ability to respond to the current climate crisis and make
 66 decisions that are viable in the long term. Furthermore, understanding how temperature
 67 affects individual species is the first step towards understanding how temperature impacts
 68 the community dynamics (Hegel *et al.*, 2010; Cunningham *et al.*, 2021; Carbeck *et al.*, 2022)
 69 and habitat phenology (Bunnell *et al.*, 2011; Duncan *et al.*, 2012; Merkle *et al.*, 2016; Slatyer
 70 *et al.*, 2022; Gerlich *et al.*, 2025), and how these changes will impact mammals in the com-
 71 ing decades (Sobie *et al.*, 2021; Eum *et al.*, 2023; Weststrate *et al.*, 2024). We discuss the
 72 consequences of our findings at the individual, population, and community levels, and we
 73 also provide directions for future research and solutions for overcoming some common data
 74 limitations.

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)	2011-03-02	2018-01-03	200,561	13.00	146	131
Caribou (southern mountain)	1998-03-20	2009-06-06	27,921	6.00	22	20
Cougars	2006-02-04	2021-07-12	80,650	2.00	29	29

Species	Start	End	n	Δt (hours)	Animals	Has speed
Elk	2007-01-13	2013-11-19	875,853	2.00	169	169
Grizzly bears	2004-09-29	2009-09-07	39,021	1.00	18	18
Mountain goats	2019-06-24	2023-10-04	65,452	6.25	11	10
Wolves	2013-01-26	2017-08-29	202,433	0.25	39	39

75 2 Methods

76 2.1 Datasets used

77 In this study, we estimate how temperature affected mammals' probability of moving,
 78 speed when moving, and habitat selection by leveraging three datasets: (1) a multi-species
 79 collection of 25 years of GPS telemetry data throughout a large spatial range of western
 80 Canada (Fig. 1), (2) historical, hourly air temperature data from the ERA5 reanalyzed
 81 dataset (Hersbach *et al.*, 2023), and (3) temporally static rasters of percent forest cover,
 82 elevation, and distance from water. We then forecast each species' movement behaviour
 83 throughout the 21st century using monthly climate change projections under four Shared
 84 Socioeconomic Pathways (SSPs; Riahi *et al.*, 2017; Mahony *et al.*, 2022): SSP 1-2.6 ("Sus-
 85 tainability – Taking the Green Road"; low challenges to mitigation and adaptation), SSP
 86 2-4.5 ("Middle of the Road: medium challenges to mitigation and adaptation"), SSP 3-7.0
 87 ("Regional Rivalry – A Rocky Road"; high challenges to mitigation and adaptation), and
 88 SSP 5-8.5 ("Fossil-fueled Development – Taking the Highway"; high challenges to mitigation,
 89 low challenges to adaptation).

90 We acknowledge that our models of habitat selection ignore many important variables of
 91 habitat selection (e.g., forest type, structure, and age; terrain slope and aspect; prey avail-
 92 ability; population density). We limited our models to only use three simple and temporally
 93 static rasters to produce simple and easily interpretable estimates and forecasts under the
 94 assumption of temporally invariant landscapes. See the discussion section for additional
 95 detail on the advantages and limitations of using such simple models.

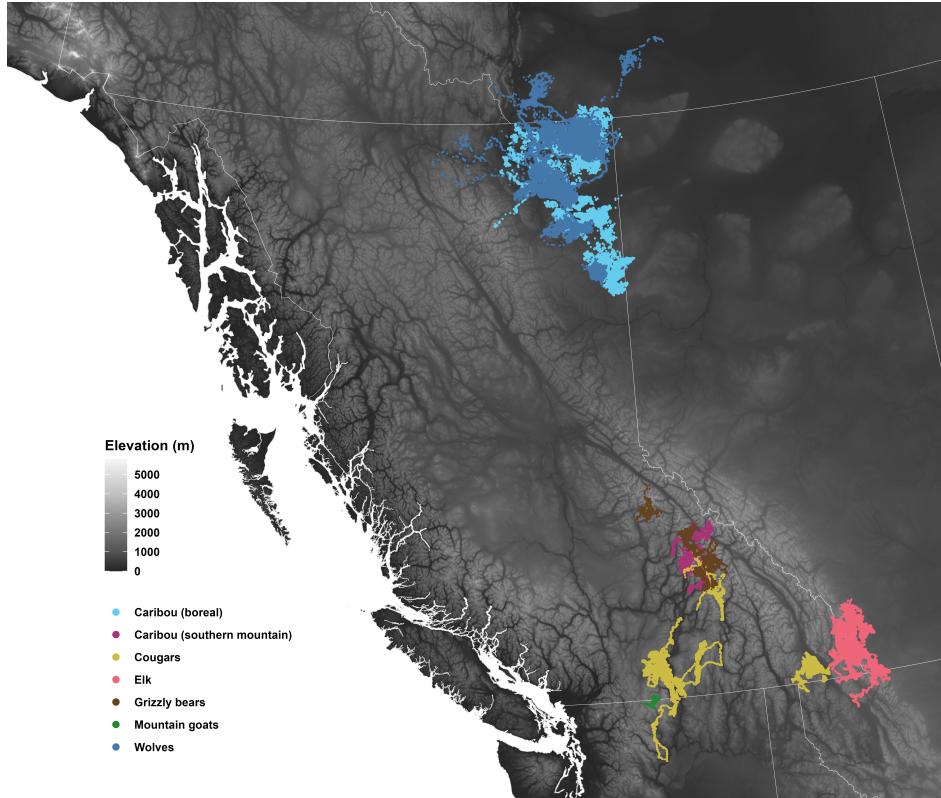


Figure 1: GPS telemetry data for the six species in this study (dots) over a digital elevation model for the study area.

96 2.1.1 GPS telemetry data

97 Boreal caribou and wolf telemetries were acquired from a data repository of the British
 98 Columbia Oil and Gas Research and Innovation Society (BC ORGIS) that was collected as
 99 part of the boreal caribou radio-collaring program of the BC OGRIS Research and Effective-
 100 ness Monitoring Board (REMB; BC OGRIS, 2018). Southern mountain caribou data were
 101 obtained from the work of Ford *et al.* (2023). Cougar data include telemetries from Dar-
 102 lington *et al.* (2025) and (serrouya_ref?). Elk data from the work of Ciuti *et al.* (2012)
 103 were downloaded from Movebank (Kays *et al.*, 2022). **MISSING INFO ON GRIZZLY**
 104 **BEAR AND GOAT TELEMETRY DATA.**

105 From the full set of telemetry data, we removed a total of 2396 problematic GPS locations
 106 (0.16%, including collar calibration data) after inspecting diagnostic plots of (1) distance
 107 from the median location, (2) straight-line displacement between locations, (3) turning angle,
 108 and (4) time interval between consecutive points. Particular attention was paid to points

¹⁰⁹ with large turning angles ($\gtrsim 170^\circ$) and excessively high straight-line displacement, especially
¹¹⁰ if antecedent and subsequent points indicated relatively stationary behaviour (Appendix A).

¹¹¹ **2.1.2 Historical temperature data and climate change projections**

¹¹² Rasters of hourly air temperature data were downloaded from the ERA5 database (Hers-
¹¹³ bach *et al.*, 2023) from the European Center for Medium-range Weather Forecasting server
¹¹⁴ (ECMWF; www.ecmwf.int; <https://cds.climate.copernicus.eu>). Proximal air temperature
¹¹⁵ was estimated for each location by extracting the value from the corresponding raster cell
¹¹⁶ from the temporally nearest raster using the `extract()` function from the `terra` package
¹¹⁷ (v. 1.7-46, Hijmans, 2023) for R (R Core Team, 2024).

¹¹⁸ We used the the `climatenetR` package (v. 1.0, Burnett, 2023) for R and ClimateNA (v.
¹¹⁹ 7.4.2; Wang *et al.*, 2016; Mahony *et al.*, 2022) to obtain projected average monthly tempera-
¹²⁰ tures from 2025 to 2100 at a 0.08° spatial resolution. Since the climate projections only pro-
¹²¹ vided monthly means and ranges but no measures of variance or distributional assumptions,
¹²² we used the historical data for western Canada from 1998 to 2023 (extremes included) to esti-
¹²³ mate the monthly variation in temperature, which we defined as σ_T^2 , the variance at location
¹²⁴ $\langle x, y \rangle$ in month m for each year (e.g., the variance at coordinates $\langle -119.40, 49.94 \rangle$ in April
¹²⁵ 2005). We then modeled the estimated variance using a Generalized Additive Model (GAM)
¹²⁶ for Location and Scale (GAMLS, Rigby & Stasinopoulos, 2005; Stasinopoulos & Rigby, 2007;
¹²⁷ section 7.9 in Wood, 2017) using the `mgcv` package for R (v. 1.9-1, Wood, 2017). The linear
¹²⁸ predictor for the location (i.e., the mean) included smooth terms of: each year's estimated
¹²⁹ within-pixel monthly mean temperature ($\hat{\mu}_T$), month (m), a two-dimensional smooth of spa-
¹³⁰ tial coordinates $\langle x, y \rangle$, and a tensor product interaction term of month and space to allow
¹³¹ for seasonal terms to vary smoothly over space. The linear predictor for the scale term,
¹³² which governs the mean-variance relationship (table 3.1 on p. 104 of Wood, 2017), included
¹³³ smooth terms of the monthly mean temperature, month, and space. We did not include
¹³⁴ smooth terms of year to avoid unrealistic projections when extrapolating beyond past 2023.

¹³⁵ The model was thus

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

¹³⁶ where $\mu_{\sigma_T^2}$ and $\nu_{\sigma_T^2}$ indicate the location and scale parameters of the gamma distribution of
¹³⁷ 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
¹³⁸ $f_{S,j}$ indicate the j^{th} smooth functions for the location and scale parameters, respectively.
¹³⁹ To ensure the smooth functions of month, $f_{L,2}(m)$ and $f_{S,2}(m)$, joined smoothly between
¹⁴⁰ December and January, the terms use cyclic cubic spline bases. The spatial terms used two-
¹⁴¹ dimensional Duchon splines, a generalization of thin-plate regression splines (p. 221 of Wood
¹⁴² (2017)). The smoothness parameters were estimated via REstricted Maximum Likelihood
¹⁴³ (REML; p. 83 of Wood, 2017). See the Data Availability Statement for additional information
¹⁴⁴ on the code used to fit the model.

¹⁴⁵ We simulated hourly variation in future years by assuming hourly temperature followed
¹⁴⁶ a normal distribution with mean specified by the monthly `climatenetR` climate projections
¹⁴⁷ and variance as specified by the gamma GMLS. For each month within each year from
¹⁴⁸ 2025 to 2100, we simulated hourly weather by including temperatures from the 0.1 to the
¹⁴⁹ 0.9 quantiles by increments of 0.1, and we weighted each quantile proportionally to the
¹⁵⁰ (normalized) Gaussian probability density for each quantile.

¹⁵¹ 2.1.3 Resource rasters

¹⁵² We estimated percent forest cover and distance from water using the temporally static
¹⁵³ rasters created by Tuanmu & Jetz (2014). We calculated total forest cover by summing

154 the four rasters of evergreen/deciduous needle-leaf trees, evergreen broadleaf trees, deciduous
155 broadleaf trees, and mixed/other trees (raster classes 1-4, respectively). We converted
156 the raster of percent cover of open water (class 12) to a binary raster of pixels with water
157 (cover > 0%) or without water (cover = 0%) and then calculated each pixel's distance from
158 the nearest pixel with water using the `distance()` function from the `terra` package. Finally,
159 we obtained two digital elevation models using the `get_elev_raster()` function from
160 the `elevatr` package (v. 0.99.0, Hollister *et al.*, 2023). We used a raster with a zoom of 6
161 (a resolution of 0.009°) for model fitting and one with a zoom of 3 (a resolution of 0.08°)
162 for downloading climate change projections via `climatenar`. All final rasters and code are
163 available on GitHub (see the Data Availability Statement). For ease of interpretability and
164 comparison with current conditions, we assumed resources would remain constant through
165 to 2100, although we recognize that the spatial distribution of forest cover and open water
166 will likely change throughout the 21st century.

167 2.2 Estimating mammals' instantaneous speeds

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

175 Since `ctmm`'s movement models assume a single moving state with stochastic but non-zero
176 speed (Calabrese *et al.*, 2016; Noonan *et al.*, 2019a), we corrected data-informed speeds so
177 that the minimum instantaneous speed could be 0. We performed this correction by sub-
178 tracting each model's mean speed while assuming speeds were χ^2 -distributed. The function
179 we used is available on GitHub (see the Data Availability Statement). To avoid artifacts

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

184 **2.3 Estimating the effects of temperature on mammals' movement behaviour**

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

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

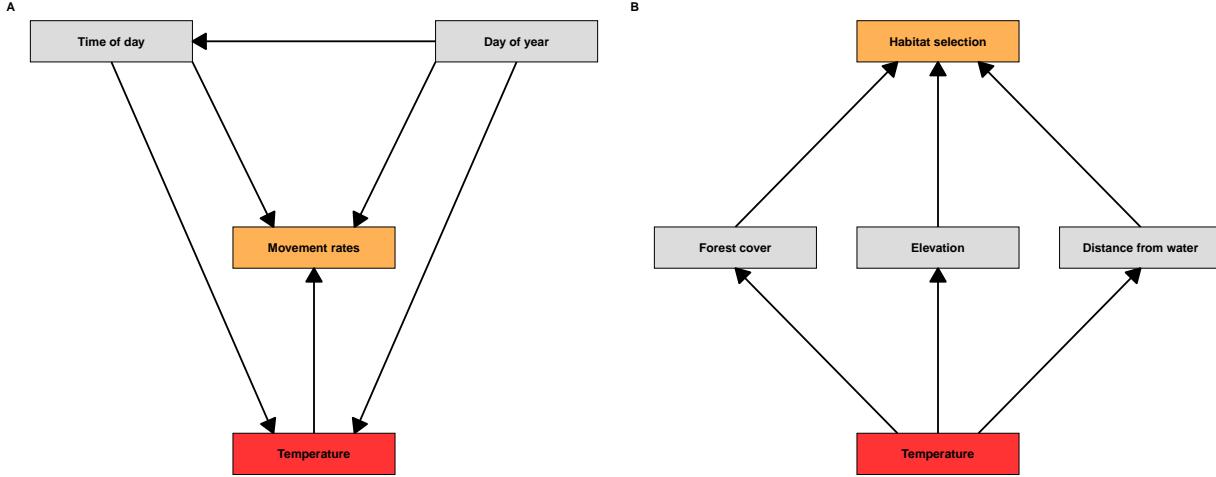


Figure 2: Directed Acyclical Graphs (DAGs) assumed for inferring the causal effects of temperature on each species' movement behaviour. (A) Ambient temperature affects mammals' movement rates (i.e. probability of moving, speed when moving, and distance traveled), but temperature is influenced by time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

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

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

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

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

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

239 **2.3.2 Effects of temperature on habitat selection**

240 We estimated the effects of temperature on each species' selection for percent forest
 241 cover (`forest_perc`), elevation (`elevation_m`, in meters), and distance from water
 242 (`dist_water_m`, in meters) by fitting a Hierarchical Resource Selection Function (HRSF) for
 243 each species (McCabe *et al.*, 2021). We fit each HRSF using an HGAM with a Poisson family
 244 of distributions and log link function (Appendix B; Aarts *et al.*, 2008). After removing
 245 non-resident individuals (Table B1), we accounted for the spatiotemporal autocorrelation
 246 in the telemetry locations by weighting each point based on the telemetry's Autocorrelated
 247 Kernel Density Estimate (Fleming & Calabrese, 2017; Noonan *et al.*, 2019b; Alston *et al.*,
 248 2022) to produce estimates of second-order habitat selection (Johnson, 1980). Quadrature
 249 points were determined using the raster cells in each animal's 99.9% AKDE percentile and
 250 given a weight of 1. The number of quadrature locations greatly outnumbered the number
 251 of observed locations (Fig. B12), especially after accounting for the AKDE weights (Fig.

252 B13).

253 Each species' model had the same structure:

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

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

267 **3 Results**

268 Of the GPS fixes with finite speed estimates, 2.6% had temperatures lower than -20°C ,
 269 while 6.5% had temperatures above 20°C , and temperature ranges differed across species
 270 (Table 2, Fig. B2). Sampling interval affected estimates of probability as well of as speed
 271 when moving (Fig. B8). Consequently, we present all results while predicting specifically
 272 for one-hour sampling intervals. At 0°C , species differed in estimated mean probabilities of
 273 moving ($\hat{P}(M = 1)$; range: 0.05 – 0.31), mean speed when moving ($\hat{\mathbb{E}}(S|M = 1)$; range:
 274 0.42 – 2.67 km/h), and mean distance traveled (i.e., $\hat{P}(M) \times \hat{\mathbb{E}}(S|M = 1)$, range: 0.04 –
 275 0.61 km/h; Table 2). Grizzly bears had the lowest movement frequency ($\hat{P}(M) \approx 0.05$),
 276 while wolves and cougars moved most often ($\hat{P}(M) \geq 0.22$). Mountain goats and southern
 277 mountain caribou moved the slowest ($\hat{\mathbb{E}}(S|M = 1) \approx 0.43$ km/h), while wolves had the
 278 highest mean speed when moving ($\hat{\mathbb{E}}(S|M = 1) \approx 2.67$ km/h). Consequently, at 0°C , wolves
 279 traveled an average of 0.22×2.67 km/h ≈ 0.6 km/h; 2.5 to 16.7 times further than other
 280 species.

Table 2: Summary statistics for each species’ 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 ($\hat{\mathbb{E}}(S|M = 1)$; km/h), and the mean distance travelled ($\hat{P}(M = 1) \times \hat{\mathbb{E}}(S|M = 1) = \hat{\mathbb{E}}(D)$; km/h), for a sampling interval of 1 hour and a temperature T of 0°C .

Species	n	$T < -20^{\circ}\text{C}$ (%)	$T > +20^{\circ}\text{C}$ (%)	$\hat{P}(M = 1 T = 0^{\circ}\text{C})$	$\hat{\mathbb{E}}(S M = 1, T = 0^{\circ}\text{C})$	$\hat{\mathbb{E}}(D T = 0^{\circ}\text{C})$
Caribou (boreal)	187,679	6.8	7.9	0.18	0.73	0.13
Caribou (s. mountain)	26,518	1.3	3.4	0.11	0.42	0.05
Cougars	80,621	0.7	6.9	0.31	0.76	0.24
Elk	875,682	2.4	4.9	0.17	0.57	0.10
Grizzly bears	39,001	0.0	8.4	0.05	0.72	0.04
Mountain goats	65,219	0.7	2.8	0.13	0.42	0.06
Wolves	202,386	1.7	13.0	0.22	2.67	0.60
Total	1,477,106	2.6	6.5			

281 Across all species, Relative Selection Strength (RSS) was weakest for forest cover and
 282 strongest for elevation. At temperatures near 0°C , wolves selected for forest cover ($\gtrapprox 50\%$),

elevations near 1 km, and distances from water < 5 km; elk selected for intermediate forest cover ($\approx 50\%$), elevations between 1 and 2 km, and distances from water of 10-15 km; mountain goats selected for sparse forest cover (< 25%), elevations near 1.5 km, and distances 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 $\Delta AIC \leq -342$; 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 trends were highly uncertain (Fig. B8). Uncertainties around the estimated effects were generally higher at extreme temperatures due to lower data availability (Figs. B4A, B5A, and B6A).

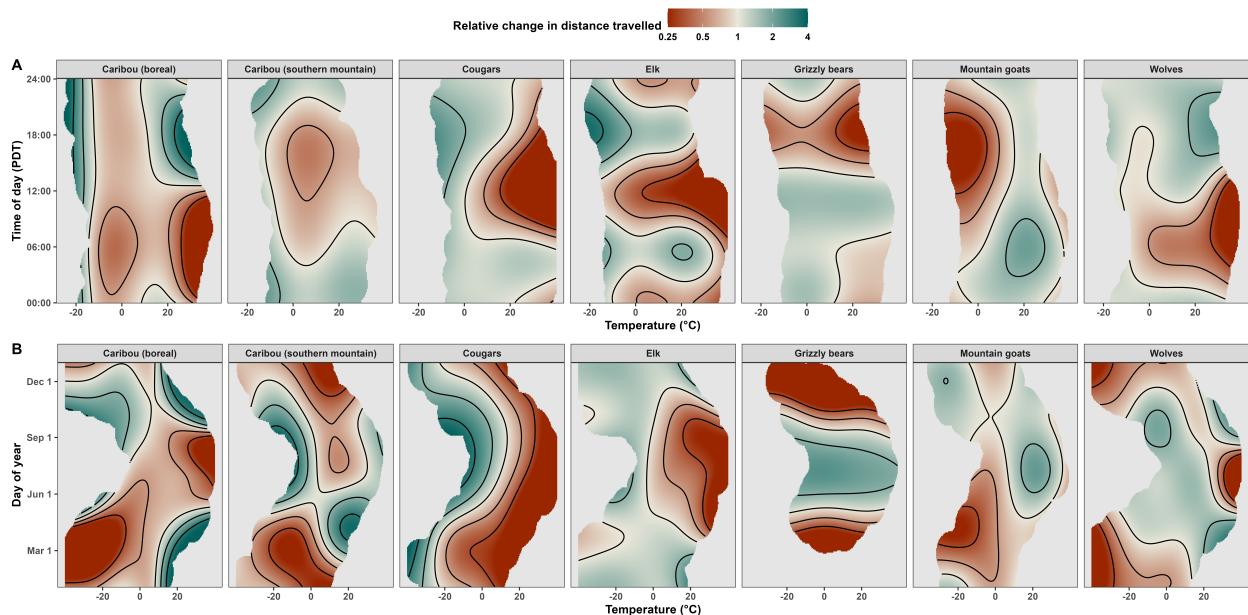


Figure 3: Temperature is a strong driver of how far and when mammals travel. The fill indicates the effects of temperature on the relative change in distance travelled (probability of moving times mean speed when moving) over time of day on June 1st (**A**) and day of year at 12:00 PDT (**B**). Predictions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

316 3.2 Effects of temperature on habitat selection

Species’ RSS was generally strongest for elevation and weakest for forest cover, but RSS depended significantly on temperature for all species (all p-values $< 2.2 \times 10^{-16}$; Fig. 4). Changes in RSS with temperature were strongest for elevation and generally weakest for distance from water, but there were no common trends across all species for any of the three resources. All species, with the exception of cougars, exhibited clear temperature-

322 dependent shifts in their preference for forest cover. At higher temperatures, wolves relaxed
 323 their preference for forested areas, while mountain goats relaxed their preference open areas
 324 (cover < 50%). As temperatures warmed, elk and boreal caribou shifted towards more forest
 325 cover closer to 50%, while southern mountain caribou and grizzly bears selected for areas with
 326 50% forest cover or less. All species shifted elevationally with temperature, although boreal
 327 caribou ha a much sharper change in RSS across elevation. Elk, mountain goats, and cougars
 328 moved to higher elevations with temperature, while wolves, southern mountain caribou, and
 329 grizzly bears moved to lower elevations. Wolves, elk, and southern mountain caribou moved
 330 closer to water with temperature, while mountain goats, cougars, and grizzly bears moved
 331 somewhat further away from water but remained mainly within 5-10 of water. As with
 332 movement rates, estimated RSS was generally most uncertain at extreme temperatures, for
 333 which data was scarcer (Fig. B15).

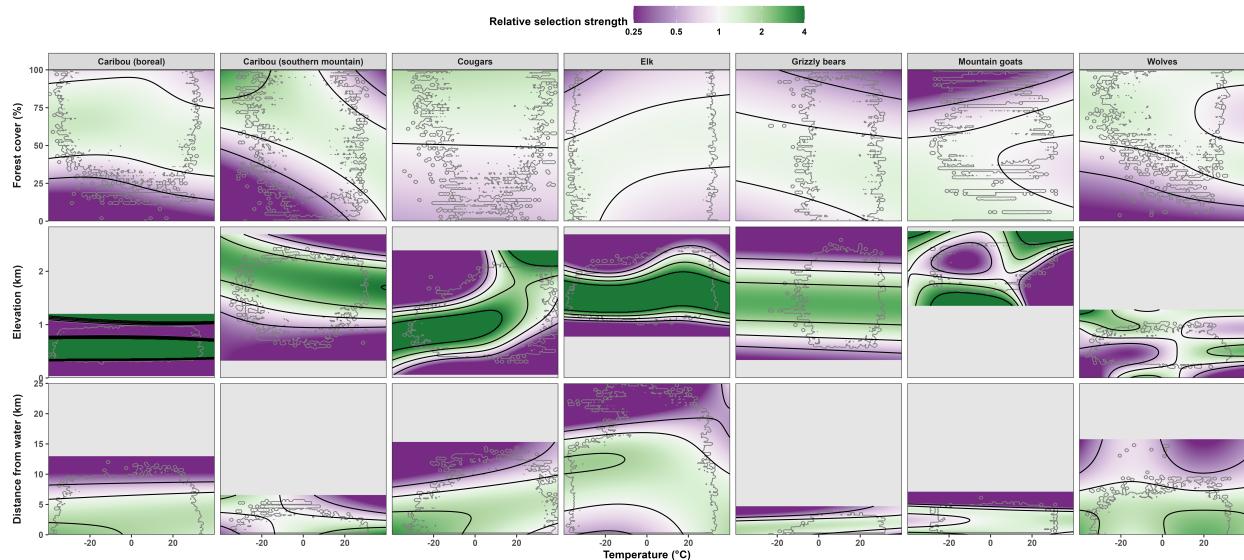


Figure 4: Mammals' habitat selection depends on ambient temperature. Estimated relative selection strength (RSS) for forest cover (%), elevation (km), and distance from water (km) as a function of temperature. The grey contours indicate the extent of each species' observed data. RSS values were re-centered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

334 3.3 Predicted changes in movement behaviour during the 21st century

335 Predicted changes in movement rates with future climate change varied across species in both
 336 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). Estimated changes in average distance travelled were negligible for boreal caribou, and grizzly bears, although both species showed seasonal changes in seasonal movement rates. As temperatures warmed, boreal caribou moved further in winter, spring, and fall but less in summer, while grizzly bears showed a clear shift towards earlier emergence from hibernation (Fig. B4) and greater movement earlier in the year but less movement in early fall. Southern mountain caribou and mountain goats are projected to travel further by 2100, although the estimates for southern mountain caribou varied greatly over space (Fig. 6). Cougars, elk, and wolves were projected to move less by 2100, with cougars showing as much as a 24% decrease in mean yearly distance travelled.

Absolute relative changes in average yearly 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). Projected changes in 2100 varied spatially due to spatial heterogeneity in climate change projections (Fig. 6). Again, absolute changes were generally greatest under worse SSPs, but the direction of change at each location also varied across SSPs (most visible in cougars).

Median RSS was projected to decrease over time within the each species' observed range, but, again, changes were stronger under worse SSPs (Fig. 7). Decreases were most pronounced in areas with the lowest RSS and most severe for elk, mountain goats, pumas, and southern mountain caribou. Changes for boreal wolves and caribou were relatively negligible. Elk, cougars, and grizzly bears were predicted to increase their selection strength for top-RSS areas, and elk, mountain goats, cougars, and southern mountain caribou were predicted to further decrease their selection for areas with low RSS. Unsurprisingly, the change in RSS between 2025 and 2100 also varied spatially for all species (Fig. 8). Overall, RSS decreased throughout most of each species' current range, although elk, cougars, and bears were predicted to increase their selection for higher-altitude habitats. Still, none of

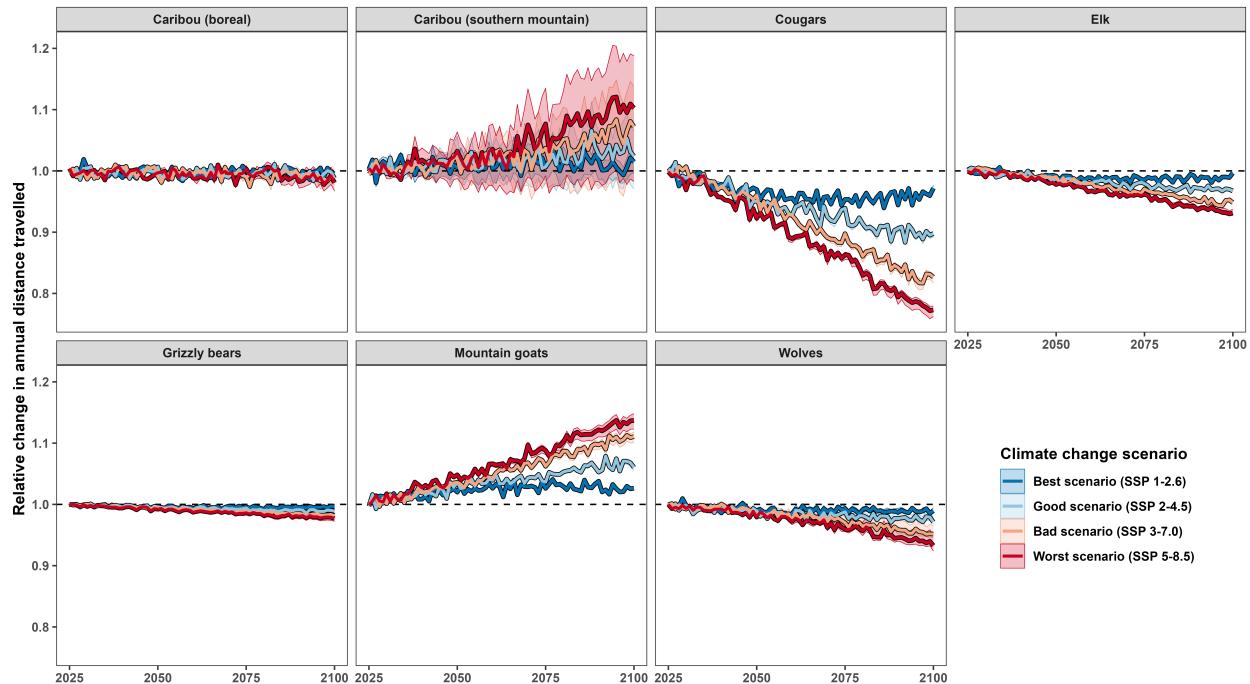


Figure 5: Species will alter their movement rates differently in response to climate change, but worse climate-change scenarios will result in the greatest change. Bold lines indicate the median change in distance travelled (probability of moving times speed when moving) due to predicted changes in temperature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

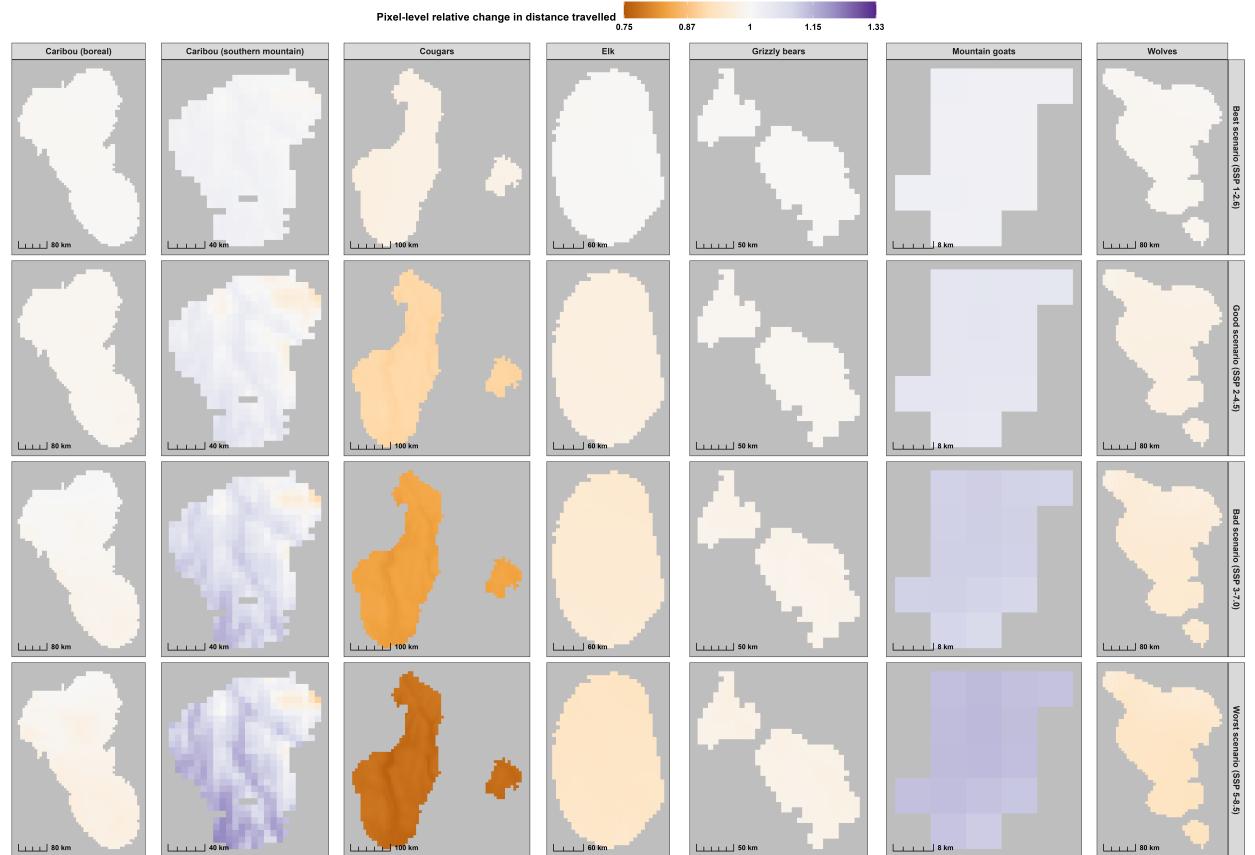


Figure 6: Climate change will impact each species' movement rates differently, but changes will also vary spatially. The color of each pixel indicates the predicted changes in distance traveled in 2100 at that pixel, relative to the value in 2025, averaged across all four scenarios. Values < 1 indicate 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 extend to each species' observed extent (Fig. 1) and are shown in the BC Albers Equal Area Conic projection (EPSG:3005).

364 the species were projected to increase RSS throughout their habitat (9).

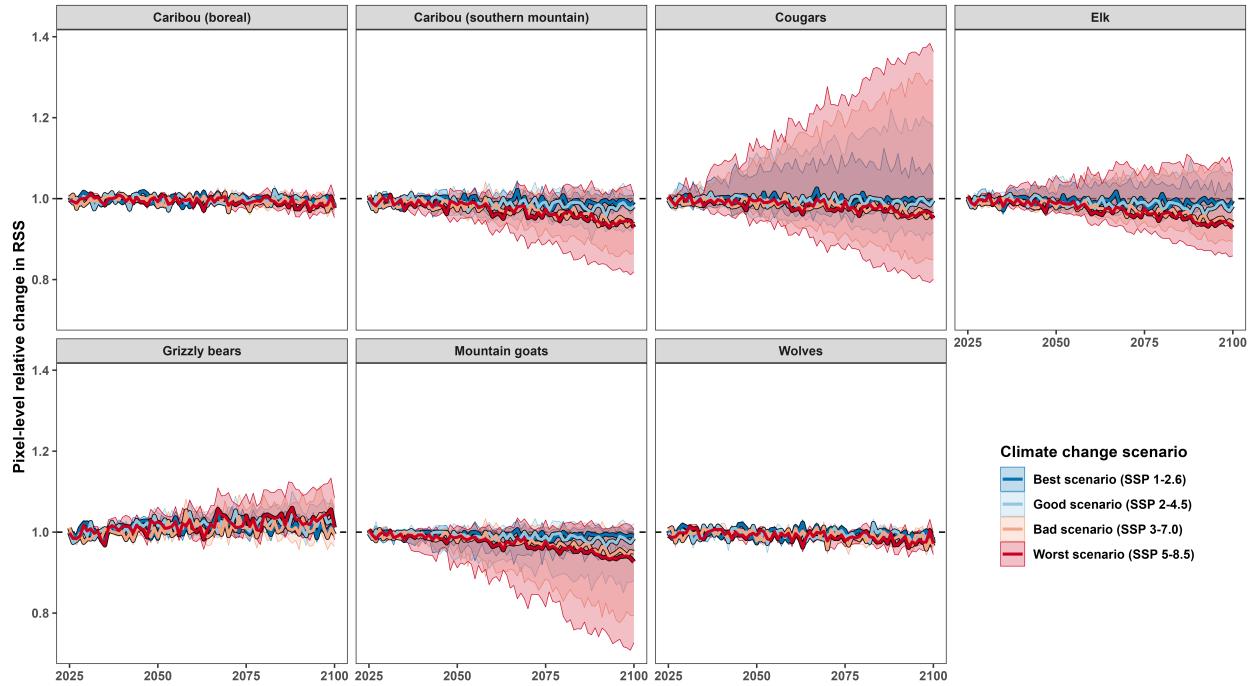


Figure 7: Species will alter their habitat selection differently in response to climate change, but worse climate-change scenarios will result in the greatest change. Bold lines indicate the change in median RSS due to predicted changes in temperature within each species' observed extent. Shaded areas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

365 4 Discussion

366 We have demonstrated that temperature is an important driver of how and where large mam-
367 mals move, and that mammals alter their seasonal and daily cycles in movement behaviour
368 in response to changes in temperature. However, predicting mammals' responses to climate
369 change remains a challenge, as habitats warm rapidly and mammals are exposed to increas-
370 ingly novel and extreme conditions (Diffenbaugh & Field, 2013; Botero *et al.*, 2015; IPCC,
371 2023). We leveraged the flexibility and interpretability of GAMs to estimate the (nonlinear)
372 responses of terrestrial mammals to temperature. In particular, tensor product interaction
373 terms were crucial for estimating smooth, nonlinear changes in daily and seasonal trends
374 with temperature. By allowing interaction terms to be smooth bivariate functions, we were



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 extend to each species' observed extent (Fig. 1) and are shown in the BC Albers Equal Area Conic projection (EPSG:3005).

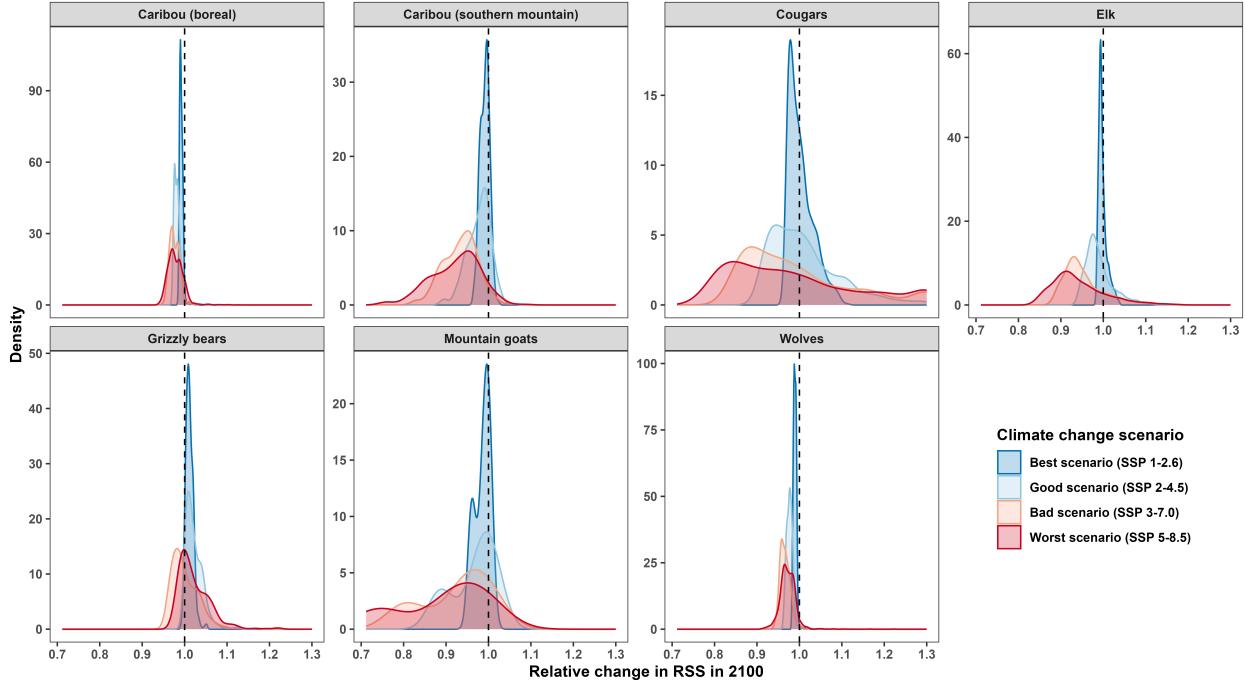


Figure 9: Climate change will cause species to decrease their selection strength for their current habitats, but worse climate change scenarios will have the greatest impact. The density plots indicate each species’ change in RSS in 2100 for their current habitat (Fig. 8), relative to each location’s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

375 able to quantify changes in movement behaviour without the need to discretize time into
 376 distinct windows (e.g., day/night and seasons). We were thus able to present changes using
 377 relatively simple and interpretable surface plots (Figs. 3 and 4) that conveyed detailed and
 378 nuanced estimates of change. This framework was essential for estimating how mammals
 379 behave in extreme conditions for which data are scarce.

380 As temperatures warm, mammals’ risk of hyperthermia increases nonlinearly (Sherwood
 381 & Huber, 2010), especially for large-bodied species (Alston *et al.*, 2020; Dyer *et al.*, 2023;
 382 Verzuh *et al.*, 2023). The recent increase in frequency and duration of extreme-temperature
 383 events (Bunnell *et al.*, 2011; Kienzle, 2018; Yao *et al.*, 2022; IPCC, 2023; Zhang *et al.*, 2023)
 384 have forced many mammals towards increasingly atypical behaviours with long-term conse-
 385 quences, ranging from changes in the behaviour and fitness of individuals (Cunningham *et*
 386 *al.*, 2021; Brivio *et al.*, 2024) to mass die-offs (Ameca y Juárez *et al.*, 2012). A species’ abil-
 387 ity to respond to changing temperature and phenology depends mainly on the its exposure,

388 sensitivity, and adaptability to changes, and growing evidence suggests that many mammals
389 in western Canada will struggle to respond due limitations in all three factors (Ameca y
390 Juárez *et al.*, 2012; Diffenbaugh & Field, 2013). Firstly, exposure to warming temperatures
391 is widespread throughout the area, and warming is expected to accelerate over the coming
392 decades (Bunnell *et al.*, 2011; Diffenbaugh & Field, 2013; Kienzle, 2018; Eum *et al.*, 2023;
393 IPCC, 2023). Secondly, large-bodied mammals are particularly sensitive to high heat (Dyer
394 *et al.*, 2023), but small-bodied mammals are also affected (Krebs *et al.*, 2019; Ratnayake
395 *et al.*, 2019). Finally, species' adaptability is tested by the speed of climate change (Diff-
396 enbaugh & Field, 2013) and the rigidity of many species' photoperiod-dependent phenology
397 (Walker *et al.*, 2019).

398 Our results suggest that climate change will cause mammals to alter their seasonal move-
399 ment behaviour, but not all species will respond similarly. For example, hotter temperatures
400 caused boreal caribou to travel longer distances in fall, winter, and spring but less in sum-
401 mer, mirroring the findings of Stien *et al.* (2012), Leclerc *et al.* (2021), and Lessard *et*
402 *al.* (2025). The increase in movement rates during the colder seasons are likely partly due
403 to shallower snow depth that results in greater mobility (Pedersen *et al.*, 2021), but rising
404 temperatures during snowy seasons also increase the chances of rain-on-snow events, which
405 limit forage availability and increase the ungulates' need to search for food (Stien *et al.*,
406 2012; Berger *et al.*, 2018; Mezzini *et al.*, 2025). In contrast, the reduced movement rates
407 during warmer summers are likely mainly due to caribou searching for shelter from the heat
408 due to ungulates' elevated risk of hyperthermia (Alston *et al.*, 2020; Verzuh *et al.*, 2023).
409 The effects of extreme temperatures are exacerbated by phenological mismatches with sea-
410 sonal photoperiod (Walker *et al.*, 2019), including the timing of molting and reproduction.
411 Earlier growth seasons in boreal and arctic regions have resulted in lower calf birth and sur-
412 vival (Post & Forchhammer, 2008), while the lengthening of the growth season has allowed
413 moose (*Alces alces*) and deer (*Odocoileus* spp.) to encroach on boreal caribou habitat, along
414 with increased density of coyotes (*Canis latrans*), cougars, and wolves (Barber *et al.*, 2018;

⁴¹⁵ DeMars *et al.*, 2023). Thus, rising temperatures affect more than each individual species'
⁴¹⁶ movement behaviour; they have complex and interconnected effects on an entire community
⁴¹⁷ and its trophic structure.

⁴¹⁸ Our results suggest that rising temperatures will have similar effects on boreal wolves.
⁴¹⁹ Warmer temperatures caused wolves to travel further throughout the year, but, similarly
⁴²⁰ to boreal caribou, they moved substantially less at temperatures above 25°C in summer.
⁴²¹ At temperatures above 20°, both boreal caribou and wolves tended to move less during the
⁴²² day and more between 17:00 and 24:00. This synchronicity in movement patterns is likely
⁴²³ to increase encounters between the two species, particularly when coupled with increasing
⁴²⁴ human disturbances, since wolves leverage seismic lines and other anthropogenic linear fea-
⁴²⁵ tures (e.g., roads) to reduce movement costs while increasing the chances of encountering
⁴²⁶ prey (Whittington *et al.*, 2011; Dickie *et al.*, 2017; Dickie *et al.*, 2022). Additionally, caribou
⁴²⁷ that attempt to reduce predation risk from wolves by avoiding wolf habitat may risk increas-
⁴²⁸ ing predation pressure from bears (Leblond *et al.*, 2016) and other encroaching predators
⁴²⁹ (DeMars *et al.*, 2023). As temperatures rise and allow new competitors and predators to
⁴³⁰ encroach on boreal caribou habitat (Barber *et al.*, 2018; DeMars *et al.*, 2023; Labadie *et al.*,
⁴³¹ 2023), climate change will have complex consequences not only for individual species but for
⁴³² entire communities and their trophic interactions.

⁴³³ Considerations about changes in trophic interactions leads to an important caveat about
⁴³⁴ the results we present. The estimated effects of temperature on movement behaviour cannot
⁴³⁵ be fully attributed to physiological responses to changes in temperature alone, since other
⁴³⁶ aspects of habitats' seasonal phenology are (nonlinearly) correlated with temperature. For
⁴³⁷ example, mountain goats' reduced movement rates at temperatures near 0°C in winter may
⁴³⁸ be due to increased movement difficulty, since melting snow and rain-on-snow events affect
⁴³⁹ the energetic costs of movement (White, 2025) and encounter rates with predators (Sullender
⁴⁴⁰ *et al.*, 2023). However, milder temperatures can also increase plant growth, which, in turn,
⁴⁴¹ allows goats to spend less time searching for forage (White *et al.*, 2025). Therefore, the

442 figure 3 illustrates an estimate of the total effect of temperature on each species movement
443 rates, but it does not explicitly account for energetic costs. Similarly, species' changes in
444 habitat selection do not explicitly account for any changes in physiological or energetic costs.
445 Both mountain goats and elk selected for higher elevation as temperatures warmed, but our
446 models did not explicitly account for differences in forage availability at different altitudes.

447 Forage quality and availability is often a limiting factor for mammals' ability to adapt
448 to warming temperatures by moving to higher altitudes. Plants are slower to arrive in and
449 establish in new habitats than mammals, and the advance of herbivores can further limit
450 plants' ability to establish (Speed *et al.*, 2012; Diffenbaugh & Field, 2013). Consequently,
451 mammals that move to higher elevations may be forced to spend more time foraging (Mezzini
452 *et al.*, 2025), which will increase their energetic expenditure as well as their chances of en-
453 countering predators (including cougars and grizzly bears) or competitors (Kohl *et al.*, 2019;
454 Martinez-Garcia *et al.*, 2020; Tórrez-Herrera *et al.*, 2020; Smith *et al.*, 2023). Additionally,
455 plants at high elevations may have weaker defenses against herbivory and be more suscep-
456 tible to overgrazing (Callis-Duehl *et al.*, 2017). The scarcity and susceptibility of forage may
457 thus limit herbivores' ability to shift elevationally, particularly if predation rates remain
458 relatively unchanged or increase. Furthermore, the physical upper limit to elevation can
459 cause individuals to become trapped . If local peaks become unsuitable habitat, and moving
460 to nearby higher peaks requires traveling across low-quality and high-risk habitat (Figure
461 8), habitat fragmentation may become too excessive to move across patches or alternative
462 ranges (White *et al.*, 2025). Translocating animals to locations with higher peaks may help
463 avoid such a scenario, but the success of relocations can be highly species-dependent, and
464 attempts are not always successful (Ranc *et al.*, 2022; White *et al.*, 2025).

465 Changes in mammals' seasonal movement behaviour are also likely to affect the timing
466 and frequency of human-wildlife interactions (Abrahms *et al.*, 2023; Weststrate *et al.*, 2024).
467 Since heat affects mammals' sleep quality and likelihood to enter torpor (Fjelldal *et al.*, 2021;
468 Wells *et al.*, 2022; Mortlock *et al.*, 2024), future decades may see increased levels of incidents

⁴⁶⁹ with bears that struggle to enter or remain in hibernation (Johnson *et al.*, 2018). The risk
⁴⁷⁰ is further increased when bears' are unable to meet their increased energetic requirements
⁴⁷¹ through foraging or hunting. Projected increases in park attendance due to rising temper-
⁴⁷² atures and human population density in Western Canada are expected to further increase
⁴⁷³ frequency of human-wildlife interactions (Weststrate *et al.*, 2024).

⁴⁷⁴ **4.1 Consequences for conservation**

⁴⁷⁵ Species' adaptability to rising temperatures is challenged by the aforementioned simulta-
⁴⁷⁶ neous, multifarious, and interconnected stressors caused by climate change, since responding
⁴⁷⁷ to many concurrent changes at once is particularly difficult (Diffenbaugh & Field, 2013;
⁴⁷⁸ Polazzo *et al.*, 2024). Locations may thus not be able to support species and population
⁴⁷⁹ sizes they supported historically, and species may thus not select for historical geographical
⁴⁸⁰ ranges in the future. It is therefore crucial for conservationists and other decision-makers to
⁴⁸¹ distinguish between a species' ideal environmental space (or E space, *sensu* Matthiopoulos,
⁴⁸² 2022), and its best available geographic space (or G space, *sensu* Matthiopoulos, 2022). Ac-
⁴⁸³ celerating multifarious change in species' movement behaviour and energetic costs require
⁴⁸⁴ conservation measures to be proactive and anticipate future changes, even when future con-
⁴⁸⁵ ditions are substantially different from historical conditions and historical data may not be
⁴⁸⁶ available. To this end, the framework presented by Polazzo *et al.* (2024) for estimating
⁴⁸⁷ species' responses to multifarious change becomes essential, particularly when accounting
⁴⁸⁸ for energetic and fitness costs, as argued by Cunningham *et al.* (2021).

⁴⁸⁹ As of December 2024, only 13.8% of terrestrial Canada was within protected areas or
⁴⁹⁰ other conserved areas (Environment and Climate Change Canada, 2025), so rapid action
⁴⁹¹ is necessary to protect additional 16.2% of Canada's land by 2030 in accordance with
⁴⁹² Kunming-Montreal Global Biodiversity Framework (i.e., the "30 by 30 initiative"; Conven-
⁴⁹³ tion on Biological Diversity, 2022). However, the choice of what habitats to protect will re-
⁴⁹⁴ quire careful consideration, since protected areas should support species not only in present

495 conditions but also as species' needs and selection change over the coming decades (Simmons
496 *et al.*, 2021). As anthropogenic activity increasingly alters habitats and community struc-
497 tures (Sih *et al.*, 2011; Tucker *et al.*, 2018; Rice, 2022; Rosenthal *et al.*, 2022), protecting
498 biodiversity and the habitats it depends on will require widespread and collaboration with
499 local stakeholders, especially Indigenous Peoples, to ensure that all decisions are culturally
500 sound and respect Treaties (Turner & Clifton, 2009; Desjardins *et al.*, 2020; Wong *et al.*,
501 2020; Hessami *et al.*, 2021; Falardeau *et al.*, 2022; Lamb *et al.*, 2023). Understanding the
502 consequences of climate change in mammalian movement behaviour is a first step towards
503 proactively responding to how mammals will respond to human-induced rapid environmen-
504 tal change (Sih *et al.*, 2011; Williams & Blois, 2018). However, a better understanding of
505 such consequences will require a more holistic approach that includes careful data collection,
506 model design, and interpretation and application of results.

507 4.2 Study strengths and limitations

508 Our results demonstrate that mammals respond to changes in temperature by altering
509 how and where they move in complex and nonlinear ways (Figs. 3 and 4). Hierarchical Gen-
510 eralized Additive Models were crucial in producing such results. The hierarchical approach
511 us to produce statistically sound population-level estimates by accounting for differences in
512 behaviour and data availability across individuals (Pedersen *et al.*, 2019; Muff *et al.*, 2020;
513 McCabe *et al.*, 2021; Mortlock *et al.*, 2024; Jeltsch *et al.*, 2025; Silva *et al.*, 2025), while the
514 flexibility of GAMs estimated mammals' changes in movement behaviour without imposing
515 rigid assumptions about the shape of the responses (Simpson, 2018, 2025). Still, GAMs'
516 flexibility and complexity can be a frustrating limitation if used too generously by inexpe-
517 rienced analysts. We suggest choosing the basis size (k) for each smooth term carefully.
518 While penalized splines and REML can help avoid unruly smooth terms that would result
519 in questionable estimates the penalty terms can struggle to restrict model complexity when
520 datasets are particularly large (Wood, 2017; Wood *et al.*, 2017).

Despite the statistical soundness of the models, estimating mammals' response to projected climate change remained a challenge because climate change projections included mean monthly temperatures but no measures of the full distribution of temperature. Since mammals' responses to temperature are nonlinear, accurate estimates of the effects of climate change require estimates of the full distribution of temperatures that mammals will be exposed to – estimated means alone are not sufficient. This is because, since the responses to temperature are nonlinear, the mean response across the distribution of temperatures is not the same as the response to mean temperature. This inequality is often referred to as Jensen's inequality or the fallacy of the average (Jensen, 1906; Denny, 2019), and it is a main motivator for Generalized Linear Models and GAMs (Denny, 2017; Simpson, 2025). We approximated of the distribution of monthly temperatures by assuming monthly temperatures were normally distributed after estimating monthly variance in temperature, but more work is necessary on estimating changes in climate beyond montly mean values.

A second advantage of our approach is the use of continous-time estimates of speed and distance traveled that are less impacted by irregular sampling rates than straight-line displacement (Noonan *et al.*, 2019a). Still, our results indicate that the movement models fit by `ctmm` still suffer from two crucial issues. Firstly, although the models allow speeds to vary stochastically over time, they assume non-zero speeds and do not currently allow for multiple movement states (Auger-Méthé *et al.*, 2021). Secondly, while continuous-time estimates of speed are less sensitive to sampling rates than straight-line displacement estimates, our models indicate that longer sampling intervals still cause speed and travel distance to be underestimated (Fig. B8; also see DeNicola *et al.*, 2025). Shorter sampling intervals may help overcome this bias (Noonan *et al.*, 2019a; Nathan *et al.*, 2022; Pease, 2024). To account for the occasional missed GPS fix, we suggest setting sampling intervals to five or more times smaller than the animal's expected directional persistence (Noonan *et al.*, 2019a). Still, excessively high sampling can cause the animal's movement to be confounded with GPS error (Fleming *et al.*, 2020), so we suggest calibrating GPS error whenever possible.

548 The final (and arguably most evident) limitation of our study was the use of temporally
549 static estimates of forest cover. While the use of a single raster produced results and fore-
550 casts that are relatively simpler and easier to interpret, species' selection to estimated forest
551 cover was relatively weak. Future studies should account for temporal variation in forest
552 cover, especially given the growing severity of forest fires in Canada (Zurowski, 2023) as well
553 widespread tree harvesting and its impact on wildlife (Betts *et al.*, 2022; Lochhead *et al.*,
554 2022). Additionally, a finer spatial scale may help detect changes in forest edge selection
555 with greater precision. Future work would also benefit from accounting for other important
556 forest properties, such as age, tree composition, and canopy height. However, accounting for
557 more variables requires careful consideration about what values such variables should take
558 when estimating changes in movement behaviour under future conditions.

559 **4.3 Considerations for future work**

560 ***HERE***

561 We have presented a multi-species analysis of the effects of temperature on mammalian
562 movement rates and habitat selection in hopes that other researchers can leverage this frame-
563 work and models to expand our understanding of how temperature affects the movement be-
564 haviour of other species, including smaller mammals, more elusive species, and non-mammal
565 animals.

566 large mammals give clear responses, but they are also already studied most often

567 More work is necessary on quantifying interspecific responses to temperature, including
568 the effects of temperature on predation rates (but see: Cunningham *et al.*, 2021; Glass *et*
569 *al.*, 2021; Brivio *et al.*, 2024). The increase in intensity and frequency of extreme heat events
570 (Bunnell *et al.*, 2011; Yao *et al.*, 2022) will likely also impact the occurrence and timing of
571 hibernation (Wells *et al.*, 2022) and migration or seasonal range expansions (Morley, 2021;
572 Carbeck *et al.*, 2022; Malpeli, 2022). However, not all species may be able to adapt at
573 the current rate of climate change (Heten *et al.*, 2014; Williams & Blois, 2018), especially

574 since landscape changes will likely depend not only on the direct effect of temperature but
575 also on cascading changes in the availability and unpredictability of resources (McLellan &
576 McLellan, 2015; Pigeon *et al.*, 2016; Mezzini *et al.*, 2025).

577 Future work should explore the effects of temperature on movement behaviour while
578 accounting for finer-scale and species specific variables that were not accounted for in this
579 study. Examples of these include temporally dynamic measures of forest type and age, canopy
580 density, competitive pressures, forage availability, and predator avoidance, or environmental
581 stochasticity. However, many of these data not available, so we also suggest that more
582 work be done on quantifying such measures using spatiotemporally dynamic models and
583 sufficiently fine resolutions. ... animals in the study are generalists; we need more work on
584 specialists (i.e., species without wide species distributions) and smaller species, but they can
585 be harder to track.

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

589 Author contributions

590 SM performed the data cleaning, ran the analyses, and wrote the manuscript. CHF wrote
591 code for estimating instantaneous movement speeds. MJN conceived of the project idea and
592 supervised SM throughout the project. All other authors contributed telemetry data and
593 reviewed the interpretation of the results for their species of interest. KH and SD contributed
594 substantially to manuscript review. All authors contributed to reviewing the manuscript.

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