

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 and community dynamics. 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 (boreal and southern mountain caribou, cougars, elk, grizzly bears, mountain goats, and wolves) throughout western Canada between 1998 and 2023. We show that temperature significantly affected of how and where these mammals moved, and we predict that climate change will impact mammals' movement behaviour throughout the 21st century, although species did not respond uniformly to temperature. Projected responses to climate change suggested that rising temperatures will drive southern mountain caribou and mountain goats to move more, while cougars, elk, and wolves will move less. Boreal caribou and grizzly bears showed little change in projected yearly movement rates but clear shifts in seasonal phenology. We also predict that rising temperatures will reduce median habitat selection strength most of the six species, but some are expected to show increased selection strength for higher altitudes. As mammals increasingly alter their movement rates and select against portions of their current ranges, changes in individuals' movement behaviour will impact encounter rates, including predator-prey dynamics and human-wildlife interactions. Conservation efforts should therefore account for future changes in movement behaviour as well as the consequences such changes may have on communities. 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;
⁶ Peterson *et al.*, 2021; Bartashevich *et al.*, 2024; Tan *et al.*, 2024). How and where animals
⁷ move thus also determines encounter rates with resources (Mezzini *et al.*, 2025), humans
⁸ (Johnson *et al.*, 2018; Weststrate *et al.*, 2024), predators, prey, and competitors (Martinez-
⁹ Garcia *et al.*, 2020; Glass *et al.*, 2021; Brivio *et al.*, 2024). However, ambient temperature
¹⁰ affects animals' movement rates by altering the energetic cost of movement and thermoreg-
¹¹ ulation (McNab, 1970; Taylor *et al.*, 1982; Brown *et al.*, 2004; Fuller *et al.*, 2016; Jahn &
¹² Seebacher, 2022), and extreme temperatures can impact animals' movement rates (Dyer *et*
¹³ *al.*, 2023), phenology (Johnson *et al.*, 2018; Carbeck *et al.*, 2022), and life history (Newediuk
¹⁴ *et al.*, 2024), and even cause physiological damage and death (Hetenem *et al.*, 2014; Powers
¹⁵ *et al.*, 2017; Ratnayake *et al.*, 2019; Schmidt *et al.*, 2020; Schwerdt *et al.*, 2024). Animals
¹⁶ may search for a short-term buffer from extreme temperatures by moving to thermal refugia
¹⁷ (Hannah *et al.*, 2014; Elmore *et al.*, 2017; Attias *et al.*, 2018; Arechavala-Lopez *et al.*, 2019;
¹⁸ Gulland *et al.*, 2022), and shelter may even be preferred over forage abundance (Hall *et al.*,
¹⁹ 2016). However, climate change during the last century (IPCC, 2023) have caused animals
²⁰ to alter how and where they move as they respond to hotter temperatures and increasingly
²¹ severe and frequent extreme-heat events (Bunnell *et al.*, 2011; IPCC, 2023).

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., 2021; Newediuk *et al.*, 2024). Mammals' homeothermy can cause them to have difficulty dissipating heat, particularly when ambient temperatures are near or above body temperature. Large-bodied mammals are most likely to alter their movement behaviour with rising temperatures, since they tend to move long distances (Merkle *et al.*, 2016), are particularly sensitive to overheating (Fuller *et al.*, 2016; Alston *et al.*, 2020; Verzuh *et al.*, 2023), and their movement rates are thus strongly limited by excessive heat (Dyer *et al.*, 2023). Global warming during the last century has resulted in milder and shorter winters, hotter and longer summers, and a greater risk of extreme-heat events (IPCC, 2023), with widespread changes in mammals' seasonal phenology, fitness, and life history (Botero *et al.*, 2015; Wells *et al.*, 2022; Newediuk *et al.*, 2024). However, behavioral responses to heat vary substantially across species depending on body size, vagility, and activity times (McCain & King, 2014; Williams & Blois, 2018). For example, warming temperatures have allowed white-tailed deer (*Odocoileus virginianus*) to shift northward, which has led to increased density of wolves (*Canis lupus*) and higher predation on caribou (*Rangifer tarandus caribou*) (Latham *et al.*, 2011; Barber *et al.*, 2018; Dickie *et al.*, 2024). Preparing for and responding to future changes will require a detailed understanding of not only how temperature affects how and where mammals move but also the cascade of effects that such changes will have at the population and community levels (Cunningham *et al.*, 2021).

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). 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 (Botero *et al.*, 2015; Sawyer *et al.*, 2019) or are physiologically incapable to do so (Sherwood & Huber, 2010; Botero *et al.*, 2015; Williams & Blois, 2018). 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; Cunningham *et al.*, 2021; Melin *et al.*, 2023), but there remains a

54 need for fine-scale estimates of the effects of temperature on mammals' movement behaviour
55 and quantitative predictions of future changes in movement behaviour.

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

Species	Start	End	n	Δt (hours)	Animals	Has speed
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
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

76 2 Methods

77 2.1 Datasets used

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

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

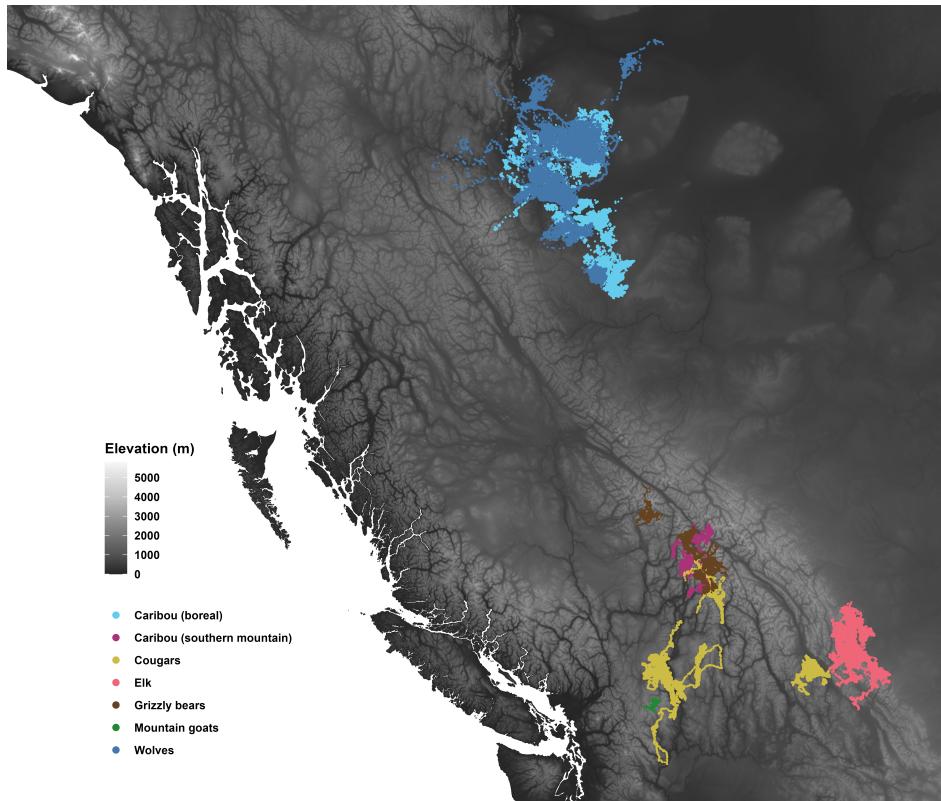


Figure 1: GPS telemetry data for the six species in this study (dots) over a digital elevation model for the study area.

96 detail on the advantages and limitations of using such simple models.

97 **2.1.1 GPS telemetry data**

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

106 From the full set of telemetry data, we removed a total of 2396 problematic GPS locations
 107 (0.16%, including collar calibration data) after inspecting diagnostic plots of (1) distance

108 from the median location, (2) straight-line displacement between locations, (3) turning angle,
109 and (4) time interval between consecutive points. Particular attention was paid to points
110 with large turning angles ($\gtrapprox 170^\circ$) and excessively high straight-line displacement, especially
111 if antecedent and subsequent points indicated relatively stationary behaviour (Appendix A).

112 2.1.2 Historical temperature data and climate change projections

113 Rasters of hourly air temperature data were downloaded from the ERA5 database (Hers-
114 bach *et al.*, 2023) from the European Center for Medium-range Weather Forecasting server
115 (ECMWF; www.ecmwf.int; <https://cds.climate.copernicus.eu>). Proximal air temperature
116 was estimated for each location by extracting the value from the corresponding raster cell
117 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 To obtain projected average monthly temperatures from 2025 to 2100 at a 0.08° spatial
120 resolution, we used the `climatenetR` package (v. 1.0, Burnett, 2023) for `R` and ClimateNA
121 v. 7.4.2 (Wang *et al.*, 2016; Mahony *et al.*, 2022). However, the climate projections only
122 included estimates of future monthly averages, a scale substantially coarser than that of our
123 tracking data (Table 1). To estimate the distribution of temperatures at an hourly scale
124 within a month, we assumed values to be approximately normally distributed with mean μ_T
125 and variance σ_T^2 . We estimated μ_T using the ClimateNA projections, while we estimated
126 σ_T^2 by modeling the observed variance in historical weather data for western Canada from
127 1998 to 2023 (inclusive). For each location $\langle x, y \rangle$ and month m of each year (e.g., the
128 observed variance at coordinates $\langle -119.40, 49.94 \rangle$ in April 2005), we calculated the variance
129 in historical temperature data, for a total of $(2024 - 1998) \times 12 = 312$ observations per
130 location. We then modeled σ_T^2 a Generalized Additive Model (GAM) for Location and Scale
131 (GAMLS, Rigby & Stasinopoulos, 2005; Stasinopoulos & Rigby, 2007; section 7.9 in Wood,
132 2017) fitted with the `mgcv` package for `R` (v. 1.9-1, Wood, 2017). The linear predictor
133 for the location (i.e., the mean) included smooth terms of: each year's estimated within-

pixel monthly mean temperature ($\hat{\mu}_T$), month (m), a two-dimensional smooth of spatial coordinates $\langle x, y \rangle$, and a tensor product interaction term of month and space to allow for seasonal terms to vary smoothly over space. The linear predictor for the scale term, which governs the mean-variance relationship (table 3.1 on p. 104 of Wood, 2017), included smooth terms of the monthly mean temperature, month, and space. We did not include smooth terms of year to avoid unrealistic projections when extrapolating beyond past 2023. The complete model for the distribution of projected temperature was thus

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

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

We simulated hourly variation in future years by assuming hourly temperature followed a normal distribution with mean specified by the monthly `climatenaR` climate projections

152 and variance as specified by the gamma GAMLS. For each month within each year from
153 2025 to 2100, we simulated hourly weather by including temperatures from the 0.1 to the
154 0.9 quantiles by increments of 0.1, and we weighted each quantile proportionally to the
155 (normalized) Gaussian probability density for each quantile.

156 **2.1.3 Habitat rasters**

157 We estimated percent forest cover and distance from water using the temporally static
158 rasters created by Tuanmu & Jetz (2014). We calculated total forest cover by summing
159 the four rasters of evergreen/deciduous needle-leaf trees, evergreen broadleaf trees, decidu-
160 ous broadleaf trees, and mixed/other trees (raster classes 1-4, respectively). We converted
161 the raster of percent cover of open water (class 12) to a binary raster of pixels with water
162 (cover > 0%) or without water (cover = 0%) and then calculated each pixel's distance from
163 the nearest pixel with water using the `distance()` function from the `terra` package. Fi-
164 nally, we obtained two digital elevation models using the `get_elev_raster()` function from
165 the `elevatr` package (v. 0.99.0, Hollister *et al.*, 2023). We used a raster with a zoom of 6
166 (a resolution of 0.009°) for model fitting and one with a zoom of 3 (a resolution of 0.08°)
167 for downloading climate change projections via `climatenar`. All final rasters and code are
168 available on GitHub (see the Data Availability Statement). For ease of interpretability and
169 comparison with current conditions, we assumed resources would remain constant through
170 to 2100, although we recognize that the spatial distribution of forest cover and open water
171 will likely change throughout the 21st century.

172 **2.2 Estimating mammals' instantaneous speeds**

173 We modeled each animal's movement using continuous-time movement models (Fleming
174 *et al.*, 2014) via the `ctmm` package (v. 1.2.0, Fleming & Calabrese, 2023) for `R`. We then
175 estimated each mammal's instantaneous speed at each observed location by applying the
176 `ctmm::speeds()` function on all models with finite speed estimates (415 of 433, Fleming *et*

¹⁷⁷ *al.*, 2014; Noonan *et al.*, 2019a). The 18 animals with insufficiently fine sampling to support
¹⁷⁸ movement models with finite speed were for one mountain goat, 15 boreal caribou, and two
¹⁷⁹ southern mountain caribou (Table 1).

¹⁸⁰ Since `ctmm`'s movement models assume a single moving state with stochastic but non-zero
¹⁸¹ speed (Calabrese *et al.*, 2016; Noonan *et al.*, 2019a), we corrected data-informed speeds so
¹⁸² that the minimum instantaneous speed could be 0. We performed this correction by sub-
¹⁸³ tracting each model's mean speed while assuming speeds were χ^2 -distributed. The function
¹⁸⁴ we used is available on GitHub (see the Data Availability Statement). To avoid artifacts
¹⁸⁵ due to excessively small, non-zero speeds, we determined whether an animal was moving or
¹⁸⁶ not using a k -means algorithm with 2 clusters for each species' distribution of detrended
¹⁸⁷ speeds. When the algorithm clearly failed to discriminate between states, we estimated the
¹⁸⁸ split point using the inflection points in histograms of the detrended speeds (Fig. B1).

¹⁸⁹ 2.3 Estimating the effects of temperature on mammals' movement behaviour

¹⁹⁰ Ambient temperature is only one of the many drivers of mammalian movement behaviour
¹⁹¹ (Fig. 2). Many species alter their movement rates (e.g., movement frequency and speed)
¹⁹² daily or seasonally in response to factors such as solar time, photoperiod, forage availability,
¹⁹³ reproductive cycles, and predator avoidance. Similarly, ambient temperature also fluctuates
¹⁹⁴ throughout the day and across seasons. Therefore, estimating the effects of temperature
¹⁹⁵ on movement rates requires accounting for how mammals' response to temperature changes
¹⁹⁶ with time of day and day of year (Fig. 2A; Péron *et al.*, 2017; Buderman *et al.*, 2018; Leclerc
¹⁹⁷ *et al.*, 2021; Xu *et al.*, 2021). Similarly, mammals' selection strength for resources depends
¹⁹⁸ on ambient temperature, since higher temperatures can promote a selection for refuge from
¹⁹⁹ heat (e.g., thicker forest cover, higher elevation, proximity to water; Attias *et al.*, 2018;
²⁰⁰ Giroux *et al.*, 2023).

²⁰¹ To assess the importance of including temperature as an explicit covariate (as opposed
²⁰² to including its effects with time of day and day of year), we fit models with and without

smooth effects of temperature and compared the fits of the two sets of models via analyses of deviance (a form of generalized likelihood ratio tests) following the methods of Section 3.3 in Wood (2017). See Appendix B for additional information.

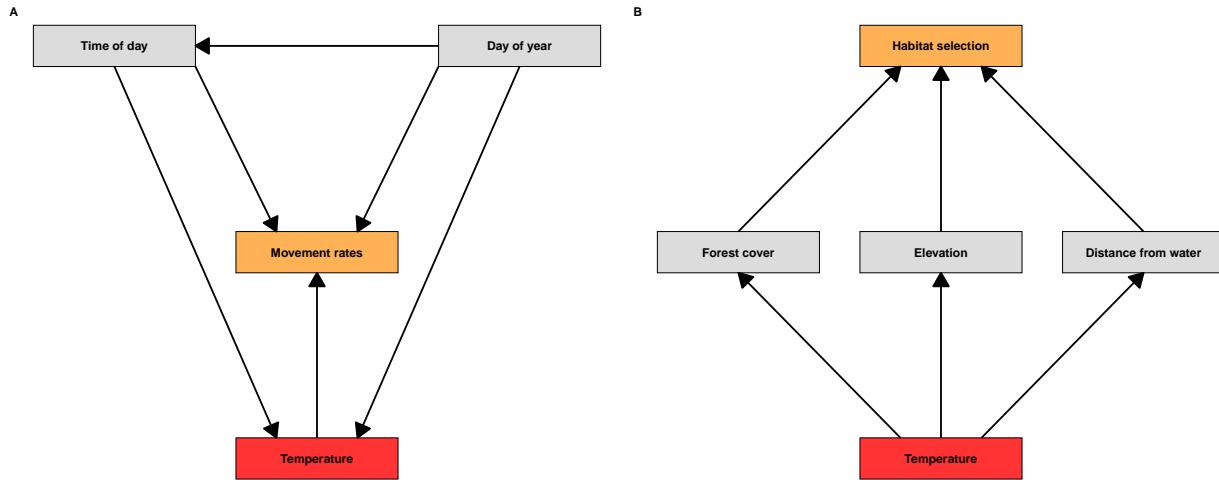


Figure 2: Directed Acyclical Graphs (DAGs) assumed for inferring the causal effects of temperature on each species' movement behaviour. (A) Ambient temperature affects mammals' movement rates (i.e. probability of moving, speed when moving, and distance traveled), but temperature is influenced by time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

216 and the gamma HGAM inform us on an animal's long-term average speed, since it is the
217 product of the probability of moving and its average speed when moving.

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

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

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

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

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

242 2.3.2 Effects of temperature on habitat selection

243 We estimated the effects of temperature on each species' selection for percent forest
 244 cover (`forest_perc`), elevation (`elevation_m`, in meters), and distance from water

245 (`dist_water_m`, in meters) by fitting a Hierarchical Resource Selection Function (HRSF) for
 246 each species (McCabe *et al.*, 2021). We fit each HRSF using an HGAM with a Poisson family
 247 of distributions and log link function (Appendix B; Aarts *et al.*, 2008). After removing
 248 non-resident individuals (Table B1), we accounted for the spatiotemporal autocorrelation
 249 in the telemetry locations by weighting each point based on the telemetry's Autocorrelated
 250 Kernel Density Estimate (Fleming & Calabrese, 2017; Noonan *et al.*, 2019b; Alston *et al.*,
 251 2022) to produce estimates of second-order habitat selection (Johnson, 1980). Quadrature
 252 points were used to approximate the likelihood function of a Poisson point process through
 253 Monte-Carlo Markov chain-based integration (Aarts *et al.*, 2008; Fithian & Hastie, 2013;
 254 Baddeley *et al.*, 2015) and were determined using the raster cells in each animal's 99.9%
 255 AKDE percentile, with each raster cell having a weight of 1. The number of quadrature
 256 locations greatly outnumbered the number of observed locations (Fig. B12), especially after
 257 accounting for the AKDE weights (Fig. B13).

258 Each species' model had the same structure:

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

259 where O indicates whether an animal was observed ($O = 1$) or not ($O = 0$), and the
 260 species-level indices are omitted for readability, but each term in the model can be as-
 261 sumed to be species-specific. Smooth effects of percent forest cover (`forest_perc`), eleva-
 262 tion (`elevation_m`, in meters), and distance to water (`dist_water_m`, in meters) accounted

for the species-level selection strength for each resource. A Gaussian random effect for each individual animal (Z_a) corrected for uneven sampling across individuals, while factor-smooth interaction terms for each animal ($f_{j,a}$) accounted for animal-level resource selection (i.e., individual-level deviations from the species-level estimate; Jeltsch *et al.*, 2025). Tensor product interaction terms of the three resources and temperature (`temp_c`) estimated the smooth change in resource selection at different temperatures. Finally, marginal smooth terms of temperature and factor-smooth interaction terms of temperature and animal accounted for species- and individual-level sampling biases at different temperatures (e.g., sampling more during warm periods).

3 Results

Of the GPS fixes with finite speed estimates, 2.6% had temperatures lower than -20°C , while 6.5% had temperatures above 20°C , and temperature ranges differed across species (Table 2, Fig. B2). Sampling interval affected estimates of probability as well of as speed when moving (Fig. B8). Consequently, we present all results while predicting specifically for one-hour sampling intervals. At 0°C , species differed in estimated mean probabilities of moving ($\hat{P}(M = 1)$; range: 0.05 – 0.31), mean speed when moving ($\hat{\mathbb{E}}(S|M = 1)$; range: 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 – 0.61 km/h; Table 2). Grizzly bears had the lowest movement frequency ($\hat{P}(M) \approx 0.05$), while wolves and cougars moved most often ($\hat{P}(M) \geq 0.22$). Mountain goats and southern mountain caribou moved the slowest ($\hat{\mathbb{E}}(S|M = 1) \approx 0.43$ km/h), while wolves had the highest mean speed when moving ($\hat{\mathbb{E}}(S|M = 1) \approx 2.67$ km/h). Consequently, at 0°C , wolves traveled an 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 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			

286 Across all species, Relative Selection Strength (RSS) was weakest for forest cover and
 287 strongest for elevation. At temperatures near 0°C , wolves selected for forest cover ($\gtrapprox 50\%$),
 288 elevations near 1 km, and distances from water < 5 km; elk selected for intermediate forest
 289 cover ($\approx 50\%$), elevations between 1 and 2 km, and distances from water of 10-15 km;
 290 mountain goats selected for sparse forest cover ($< 25\%$), elevations near 1.5 km, and distances
 291 from water < 5 km; cougars selected for dense forest cover ($> 75\%$), an elevation of ~ 1 km,
 292 and distances from water < 7.5 km; boreal caribou selected for forest cover between 50% and
 293 75%, elevations near 500 m, and distances from water < 10 km; southern mountain caribou
 294 selected for dense forest cover, elevations near 2 km, and distances from water $\lessapprox 5$ km; and
 295 grizzly bears selected for relatively sparse forest cover (25-50%), elevation between 1 and 2
 296 km, and distances from water < 3 km.

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

302 produced a better fit.

303 **3.1 Effects of temperature on movement rates**

304 Species' changes in movement rates to temperature varied in both direction and magnitude
305 (Figs. 3, B4-B6), even after accounting for differences in daily and seasonal activity (e.g.,
306 sleeping, migration, hibernation; Figs. B4-B6). Smooth interaction terms were well-behaved
307 and indicated clear shifts in activity over time of day and day of year for all species. The
308 models had good in-sample prediction (Fig. B7) and explained reasonably high proportions
309 of the deviance [79.3% for the gamma model and 10.7% for the binomial model, which
310 is relatively high for a binomial model with binary responses]. All species altered their
311 daily and seasonal movement behaviour to changes in temperature (Fig. 3). The clearest
312 example of this was cougars. In late spring (June 1st), they moved from evening to early
313 morning if temperatures were below 20°C, but if temperatures were above 20°C they moved
314 mostly between 3:00 and 6:00 AM. Throughout the year, they tended to move more when
315 it was colder, but what they perceived as "colder" was relative to the time of year. All
316 species' estimated probability of moving and speed when moving decreased with sampling
317 intervals above 1 hour, except for cougars' speed, although the estimated trends were highly
318 uncertain (Fig. B8). Uncertainties around the estimated effects were generally higher at
319 extreme temperatures due to lower data availability (Figs. B4A, B5A, and B6A).

320 **3.2 Effects of temperature on habitat selection**

321 Species' RSS was generally strongest for elevation and weakest for forest cover, but RSS
322 depended significantly on temperature for all species (all p-values < 2.2×10^{-16} ; Fig. 4).
323 Changes in RSS with temperature were strongest for elevation and generally weakest for
324 distance from water, but there were no common trends across all species for any of the
325 three resources. All species, with the exception of cougars, exhibited clear temperature-
326 dependent shifts in their preference for forest cover. At higher temperatures, wolves relaxed

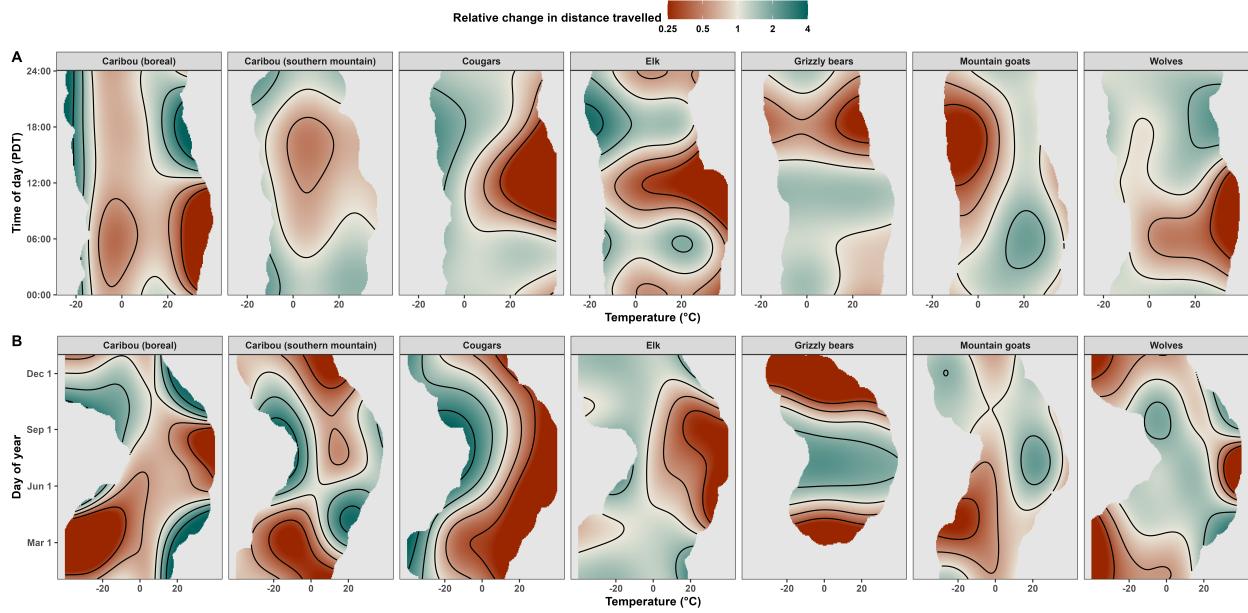


Figure 3: Temperature is a strong driver of how far and when mammals travel. The fill indicates the effects of temperature on the relative change in distance travelled (probability of moving times mean speed when moving) over time of day on June 1st (**A**) and day of year at 12:00 PDT (**B**). Predictions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

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

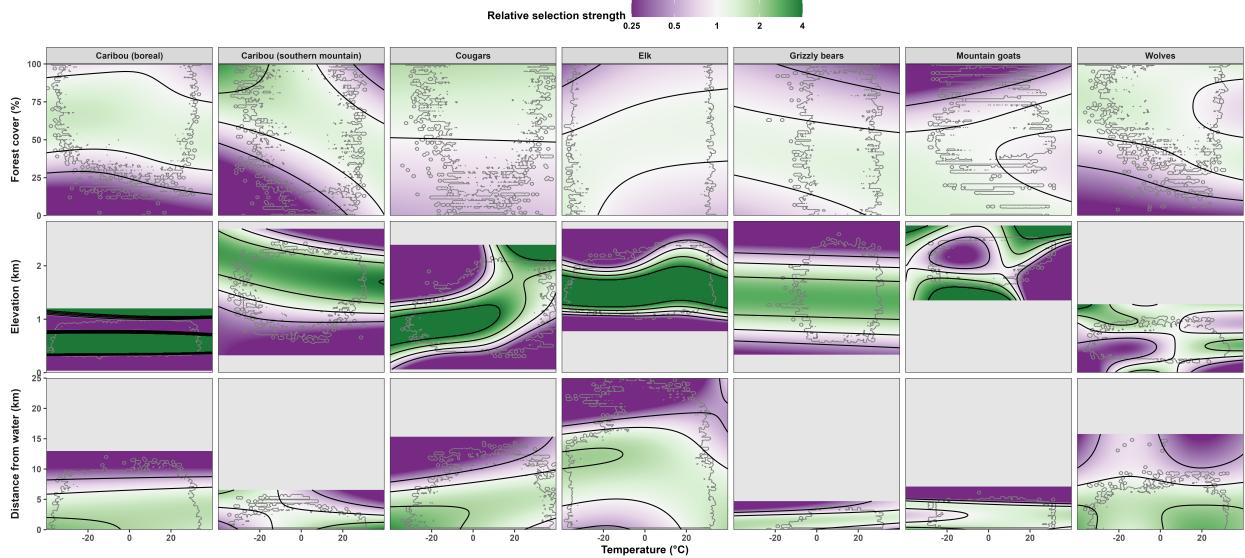


Figure 4: Mammals’ habitat selection depends on ambient temperature. Estimated relative selection strength (RSS) for forest cover (%), elevation (km), and distance from water (km) as a function of temperature. The grey contours indicate the extent of each species’ observed data. RSS values were re-centered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

338 3.3 Predicted changes in movement behaviour during the 21st century

339 Predicted changes in movement rates with future climate change varied across species in both
 340 magnitude and direction, but worse SSPs always corresponded to greater absolute changes
 341 (Fig. 5). Additionally, species that were predicted to move less often did not necessarily
 342 have lower speeds when moving, and vice versa (Figs. B9 and B10). Estimated changes
 343 in average distance travelled were negligible for boreal caribou, and grizzly bears, although
 344 both species showed seasonal changes in seasonal movement rates. As temperatures warmed,
 345 boreal caribou moved further in winter, spring, and fall but less in summer, while grizzly
 346 bears showed a clear shift towards earlier emergence from hibernation (Fig. B4) and greater
 347 movement earlier in the year but less movement in early fall. Southern mountain caribou
 348 and mountain goats are projected to travel further by 2100, although the estimates for
 349 southern mountain caribou varied greatly over space (Fig. 6). Cougars, elk, and wolves were
 350 projected to move less by 2100, with cougars showing as much as a 24% decrease in mean
 351 yearly distance travelled.

352 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).

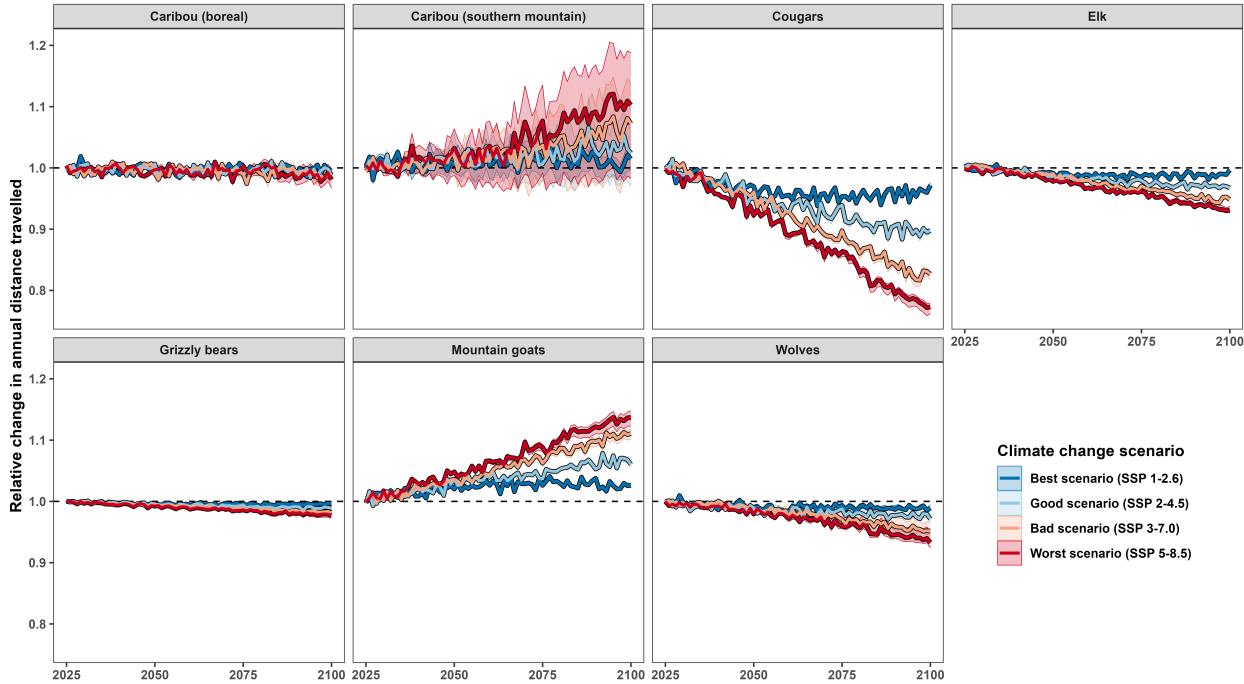


Figure 5: Species will alter their movement rates differently in response to climate change, but worse climate-change scenarios will result in the greatest change. Bold lines indicate the median change in distance travelled (probability of moving times speed when moving) due to predicted changes in temperature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

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

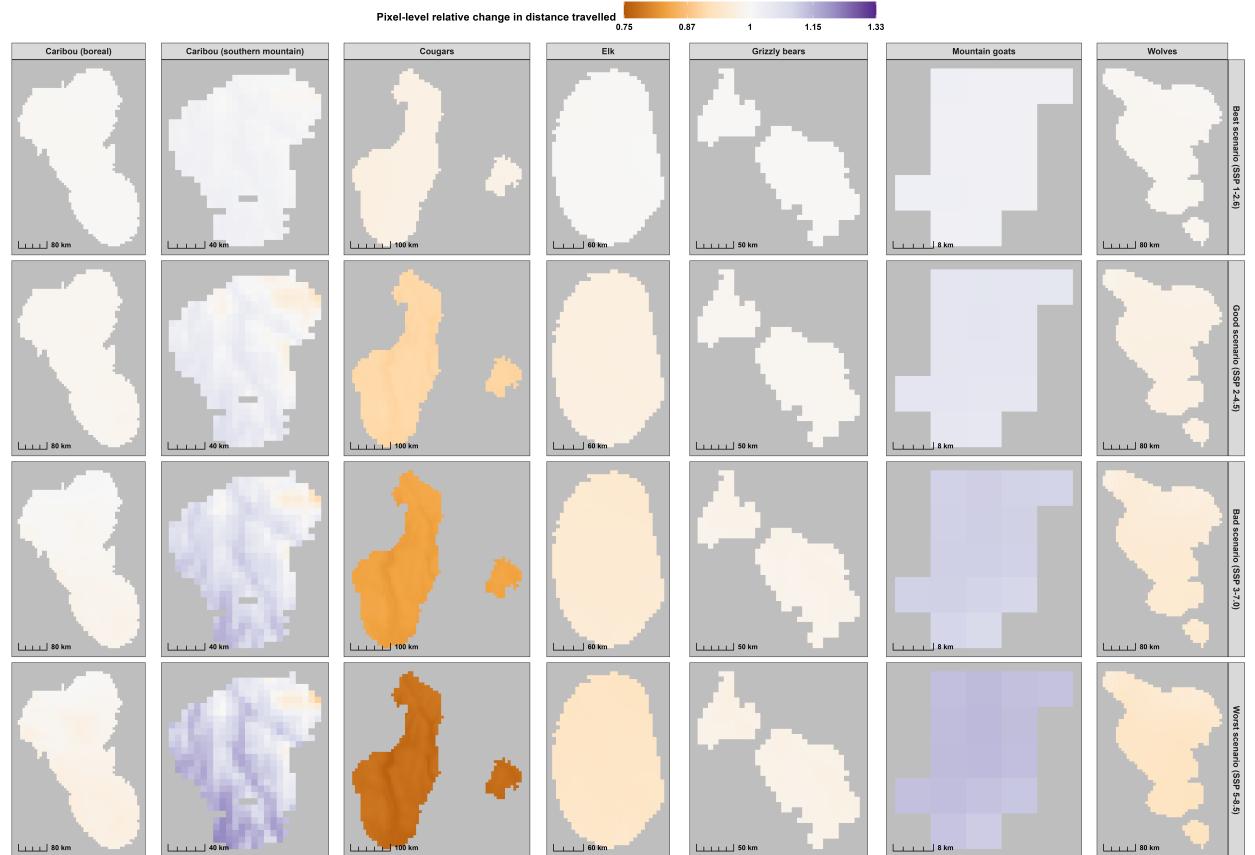


Figure 6: Climate change will impact each species' movement rates differently, but changes will also vary spatially. The color of each pixel indicates the predicted changes in distance traveled in 2100 at that pixel, relative to the value in 2025, averaged across all four scenarios. Values < 1 indicate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

365 change in RSS between 2025 and 2100 also varied spatially for all species (Fig. 8). Overall,
 366 RSS decreased throughout most of each species' current range, although elk, cougars, and
 367 bears were predicted to increase their selection for higher-altitude habitats. Still, none of
 368 the species were projected to increase RSS throughout their habitat (9).

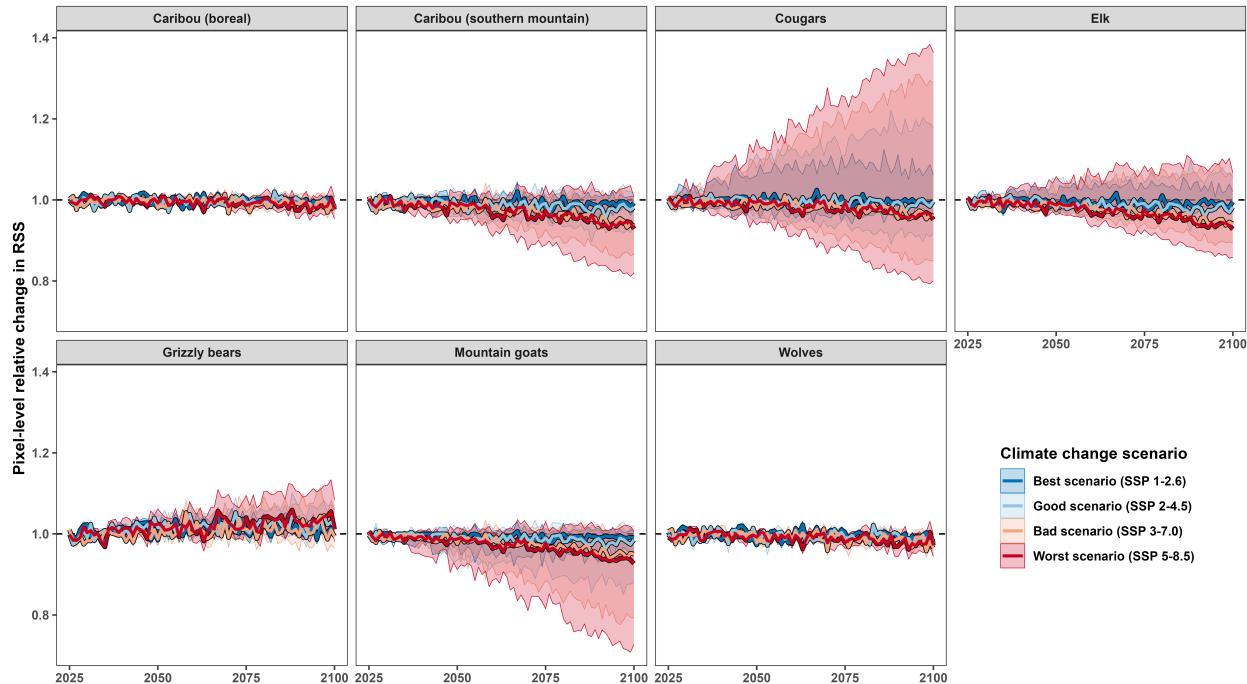


Figure 7: Species will alter their habitat selection differently in response to climate change, but worse climate-change scenarios will result in the greatest change. Bold lines indicate the change in median RSS due to predicted changes in temperature within each species' observed extent. Shaded areas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

369 4 Discussion

370 Points to add:

- 371 • thermal landscape?
- 372 • common trends:
 - 373 – boreal species do not see much of a change in distance traveled, but this is in part
 - 374 due to opposite trends in the different seasons.



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).

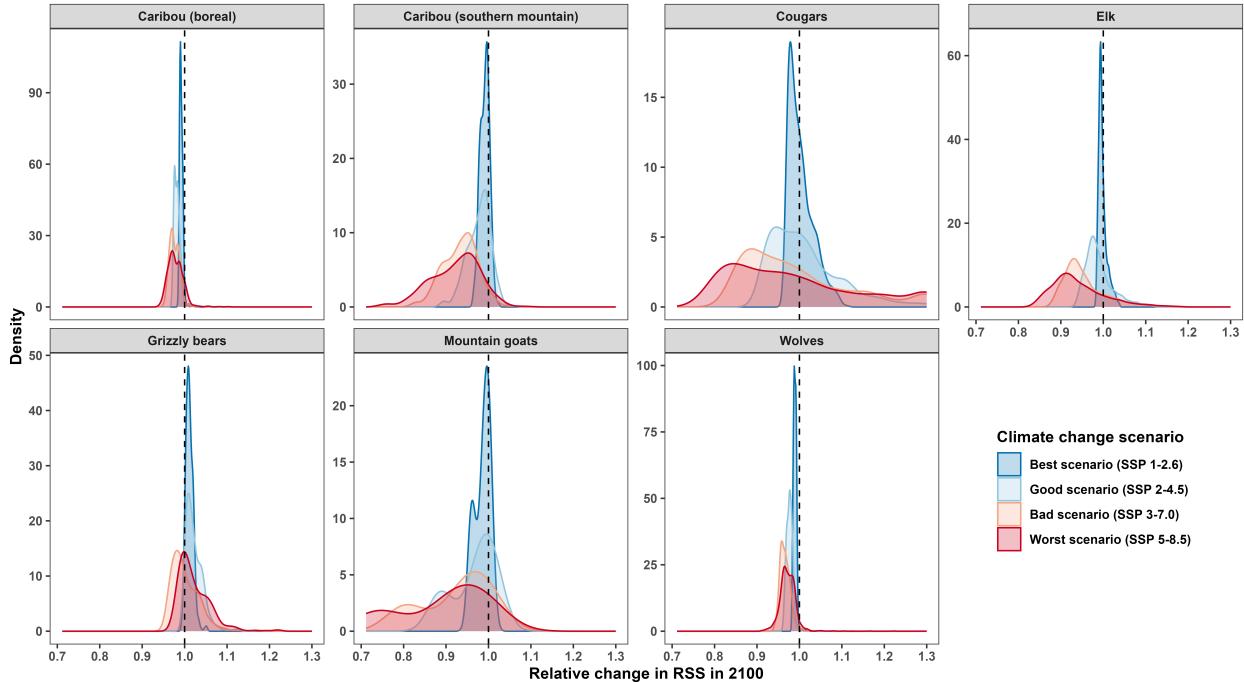


Figure 9: Climate change will cause species to decrease their selection strength for their current habitats, but worse climate change scenarios will have the greatest impact. The density plots indicate each species' change in RSS in 2100 for their current habitat (Fig. 8), relative to each location's 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 – habitat selection for boreal species flattens with temperatures above 0 but
 376 strengthens near zero. Therefore, warmer summers may result in lower encounter
 377 rates as ranges widen, but warmer winters may result in increased predation
 378 risk, which may impact reproductive success (since cows are pregnant in winter)
 379 – SM caribou and mountain goats are projected to move more and see widespread
 380 decreases in their current habitats

381 We have demonstrated that temperature is an important driver of how and where large mam-
 382 mals move, and that mammals alter their seasonal and daily cycles in movement behaviour
 383 in response to changes in temperature. However, predicting mammals' responses to climate
 384 change remains a challenge, as habitats warm rapidly and mammals are exposed to increas-
 385 ingly novel and extreme conditions (Diffenbaugh & Field, 2013; Botero *et al.*, 2015; IPCC,
 386 2023). We leveraged the flexibility and interpretability of GAMs to estimate the (nonlinear)
 387 responses of terrestrial mammals to temperature. In particular, tensor product interaction

388 terms were crucial for estimating smooth, nonlinear changes in daily and seasonal trends
389 with temperature. By allowing interaction terms to be smooth bivariate functions, we were
390 able to quantify changes in movement behaviour without the need to discretize time into
391 distinct windows (e.g., day/night and seasons). We were thus able to present changes using
392 relatively simple and interpretable surface plots (Figs. 3 and 4) that conveyed detailed and
393 nuanced estimates of change. This framework was essential for estimating how mammals
394 behave in extreme conditions for which data are scarce.

395 As temperatures warm, mammals' risk of hyperthermia increases nonlinearily (Sherwood
396 & Huber, 2010), especially for large-bodied species (Alston *et al.*, 2020; Dyer *et al.*, 2023;
397 Verzuh *et al.*, 2023). The recent increase in frequency and duration of extreme-temperature
398 events (Bunnell *et al.*, 2011; Kienzle, 2018; Yao *et al.*, 2022; IPCC, 2023; Zhang *et al.*, 2023)
399 have forced many mammals towards increasingly atypical behaviours with long-term conse-
400 quences, ranging from changes in the behaviour and fitness of individuals (Cunningham *et*
401 *al.*, 2021; Brivio *et al.*, 2024) to mass die-offs (Ameca y Juárez *et al.*, 2012). A species' abil-
402 ity to respond to changing temperature and phenology depends mainly on the its exposure,
403 sensitivity, and adaptability to changes, and growing evidence suggests that many mammals
404 in western Canada will struggle to respond due to limitations in all three factors (Ameca y
405 Juárez *et al.*, 2012; Diffenbaugh & Field, 2013). Firstly, exposure to warming temperatures
406 is widespread throughout the area, and warming is expected to accelerate over the coming
407 decades (Bunnell *et al.*, 2011; Diffenbaugh & Field, 2013; Kienzle, 2018; Eum *et al.*, 2023;
408 IPCC, 2023). Secondly, large-bodied mammals are particularly sensitive to high heat (Dyer
409 *et al.*, 2023), but small-bodied mammals are also affected (Krebs *et al.*, 2019; Ratnayake
410 *et al.*, 2019). Finally, species' adaptability is tested by the speed of climate change (Diff-
411 enbaugh & Field, 2013) and the rigidity of many species' photoperiod-dependent phenology
412 (Walker *et al.*, 2019).

413 Our results suggest that climate change will cause mammals to alter their seasonal move-
414 ment behaviour, but not all species will respond similarly. For example, hotter temperatures

415 caused boreal caribou to travel longer distances in fall, winter, and spring but less in sum-
416 mer, mirroring the findings of Stien *et al.* (2012), Leclerc *et al.* (2021), and Lessard *et*
417 *al.* (2025). The increase in movement rates during the colder seasons are likely partly due
418 to shallower snow depth that results in greater mobility (Pedersen *et al.*, 2021), but rising
419 temperatures during snowy seasons also increase the chances of rain-on-snow events, which
420 limit forage availability and increase the ungulates' need to search for food (Stien *et al.*,
421 2012; Berger *et al.*, 2018; Mezzini *et al.*, 2025). In contrast, the reduced movement rates
422 during warmer summers are likely mainly due to caribou searching for shelter from the heat
423 due to ungulates' elevated risk of hyperthermia (Alston *et al.*, 2020; Verzuh *et al.*, 2023).
424 The effects of extreme temperatures are exacerbated by phenological mismatches with sea-
425 sonal photoperiod (Walker *et al.*, 2019), including the timing of molting and reproduction.
426 Earlier growth seasons in boreal and arctic regions have resulted in lower calf birth and sur-
427 vival (Post & Forchhammer, 2008), while the lengthening of the growth season has allowed
428 moose (*Alces alces*) and deer (*Odocoileus* spp.) to encroach on boreal caribou habitat, along
429 with increased density of coyotes (*Canis latrans*), cougars, and wolves (Barber *et al.*, 2018;
430 DeMars *et al.*, 2023). Thus, rising temperatures affect more than each individual species'
431 movement behaviour; they have complex and interconnected effects on an entire community
432 and its trophic structure.

433 Our results suggest that rising temperatures will have similar effects on boreal wolves.
434 Warmer temperatures caused wolves to travel further throughout the year, but, similarly
435 to boreal caribou, they moved substantially less at temperatures above 25°C in summer.
436 At temperatures above 20°, both boreal caribou and wolves tended to move less during the
437 day and more between 17:00 and 24:00. This synchronicity in movement patterns is likely
438 to increase encounters between the two species, particularly when coupled with increasing
439 human disturbances, since wolves leverage seismic lines and other anthropogenic linear fea-
440 tures (e.g., roads) to reduce movement costs while increasing the chances of encountering
441 prey (Whittington *et al.*, 2011; Dickie *et al.*, 2017; Dickie *et al.*, 2022). Additionally, caribou

442 that attempt to reduce predation risk from wolves by avoiding wolf habitat may risk increasing
443 predation pressure from bears (Leblond *et al.*, 2016) and other encroaching predators
444 (DeMars *et al.*, 2023). As temperatures rise and allow new competitors and predators to
445 encroach on boreal caribou habitat (Barber *et al.*, 2018; DeMars *et al.*, 2023; Labadie *et al.*,
446 2023), climate change will have complex consequences not only for individual species but for
447 entire communities and their trophic interactions.

448 Considerations about changes in trophic interactions leads to an important caveat about
449 the results we present. The estimated effects of temperature on movement behaviour cannot
450 be fully attributed to physiological responses to changes in temperature alone, since other
451 aspects of habitats' seasonal phenology are (nonlinearly) correlated with temperature. For
452 example, mountain goats' reduced movement rates at temperatures near 0°C in winter may
453 be due to increased movement difficulty, since melting snow and rain-on-snow events affect
454 the energetic costs of movement (White, 2025) and encounter rates with predators (Sullender
455 *et al.*, 2023). However, milder temperatures can also increase plant growth, which, in turn,
456 allows goats to spend less time searching for forage (White *et al.*, 2025). Therefore, the
457 figure 3 illustrates an estimate of the total effect of temperature on each species movement
458 rates, but it does not explicitly account for energetic costs. Similarly, species' changes in
459 habitat selection do not explicitly account for any changes in physiological or energetic costs.
460 Both mountain goats and elk selected for higher elevation as temperatures warmed, but our
461 models did not explicitly account for differences in forage availability at different altitudes.

462 Forage quality and availability is often a limiting factor for mammals' ability to adapt
463 to warming temperatures by moving to higher altitudes. Plants are slower to arrive in and
464 establish in new habitats than mammals, and the advance of herbivores can further limit
465 plants' ability to establish (Speed *et al.*, 2012; Diffenbaugh & Field, 2013). Consequently,
466 mammals that move to higher elevations may be forced to spend more time foraging (Mezzini
467 *et al.*, 2025), which will increase their energetic expenditure as well as their chances of en-
468 countered predators (including cougars and grizzly bears) or competitors (Kohl *et al.*, 2019;

⁴⁶⁹ Martinez-Garcia *et al.*, 2020; Tórrez-Herrera *et al.*, 2020; Smith *et al.*, 2023). Additionally,
⁴⁷⁰ plants at high elevations may have weaker defenses against herbivory and be more suscepti-
⁴⁷¹ ble to overgrazing (Callis-Duehl *et al.*, 2017). The scarcity and susceptibility of forage may
⁴⁷² thus limit herbivores' ability to shift elevationally, particularly if predation rates remain
⁴⁷³ relatively unchanged or increase. Furthermore, the physical upper limit to elevation can
⁴⁷⁴ cause individuals to become trapped . If local peaks become unsuitable habitat, and moving
⁴⁷⁵ to nearby higher peaks requires traveling across low-quality and high-risk habitat (Figure
⁴⁷⁶ 8), habitat fragmentation may become too excessive to move across patches or alternative
⁴⁷⁷ ranges (White *et al.*, 2025). Translocating animals to locations with higher peaks may help
⁴⁷⁸ avoid such a scenario, but the success of relocations can be highly species-dependent, and
⁴⁷⁹ attempts are not always successful (Ranc *et al.*, 2022; White *et al.*, 2025).

⁴⁸⁰ Changes in mammals' seasonal movement behaviour are also likely to affect the timing
⁴⁸¹ and frequency of human-wildlife interactions (Abrahms *et al.*, 2023; Weststrate *et al.*, 2024).
⁴⁸² Since heat affects mammals' sleep quality and likelihood to enter torpor (Fjelldal *et al.*, 2021;
⁴⁸³ Wells *et al.*, 2022; Mortlock *et al.*, 2024), future decades may see increased levels of incidents
⁴⁸⁴ with bears that struggle to enter or remain in hibernation (Johnson *et al.*, 2018). The risk
⁴⁸⁵ is further increased when bears' are unable to meet their increased energetic requirements
⁴⁸⁶ through foraging or hunting. Projected increases in park attendance due to rising temper-
⁴⁸⁷ atures and human population density in Western Canada are expected to further increase
⁴⁸⁸ frequency of human-wildlife interactions (Weststrate *et al.*, 2024).

⁴⁸⁹ 4.1 Consequences for conservation

⁴⁹⁰ Species' adaptability to rising temperatures is challenged by the aforementioned simulta-
⁴⁹¹ neous, multifarious, and interconnected stressors caused by climate change, since responding
⁴⁹² to many concurrent changes at once is particularly difficult (Diffenbaugh & Field, 2013;
⁴⁹³ Polazzo *et al.*, 2024). Locations may thus not be able to support species and population
⁴⁹⁴ sizes they supported historically, and species may thus not select for historical geographical

495 ranges in the future. It is therefore crucial for conservationists and other decision-makers to
496 distinguish between a species' ideal environmental space (or E space, *sensu* Matthiopoulos,
497 2022), and its best available geographic space (or G space, *sensu* Matthiopoulos, 2022). Ac-
498 celerating multifarious change in species' movement behaviour and energetic costs require
499 conservation measures to be proactive and anticipate future changes, even when future con-
500 ditions are substantially different from historical conditions and historical data may not be
501 available. To this end, the framework presented by Polazzo *et al.* (2024) for estimating
502 species' responses to multifarious change becomes essential, particularly when accounting
503 for energetic and fitness costs, as argued by Cunningham *et al.* (2021).

504 As of December 2024, only 13.8% of terrestrial Canada was within protected areas or
505 other conserved areas (Environment and Climate Change Canada, 2025), so rapid action
506 is necessary to protect additional 16.2% of Canada's land by 2030 in accordance with
507 Kunming-Montreal Global Biodiversity Framework (i.e., the "30 by 30 initiative"; Conven-
508 tion on Biological Diversity, 2022). However, the choice of what habitats to protect will re-
509 quire careful consideration, since protected areas should support species not only in present
510 conditions but also as species' needs and selection change over the coming decades (Simmons
511 *et al.*, 2021). As anthropogenic activity increasingly alters habitats and community struc-
512 tures (Sih *et al.*, 2011; Tucker *et al.*, 2018; Rice, 2022; Rosenthal *et al.*, 2022), protecting
513 biodiversity and the habitats it depends on will require widespread and collaboration with
514 local stakeholders, especially Indigenous Peoples, to ensure that all decisions are culturally
515 sound and respect Treaties (Turner & Clifton, 2009; Desjardins *et al.*, 2020; Wong *et al.*,
516 2020; Hessami *et al.*, 2021; Falardeau *et al.*, 2022; Lamb *et al.*, 2023). Understanding the
517 consequences of climate change in mammalian movement behaviour is a first step towards
518 proactively responding to how mammals will respond to human-induced rapid environmen-
519 tal change (Sih *et al.*, 2011; Williams & Blois, 2018). However, a better understanding of
520 such consequences will require a more holistic approach that includes careful data collection,
521 model design, and interpretation and application of results.

522 **4.2 Study strengths and limitations**

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

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

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

563 The final (and arguably most evident) limitation of our study was the use of temporally
564 static estimates of forest cover. While the use of a single raster produced results and fore-
565 casts that are relatively simpler and easier to interpret, species' selection to estimated forest
566 cover was relatively weak. Future studies should account for temporal variation in forest
567 cover, especially given the growing severity of forest fires in Canada (Zurowski, 2023) as well
568 widespread tree harvesting and its impact on wildlife (Betts *et al.*, 2022; Lochhead *et al.*,
569 2022). Additionally, a finer spatial scale may help detect changes in forest edge selection
570 with greater precision. Future work would also benefit from accounting for other important
571 forest properties, such as age, tree composition, and canopy height. However, accounting for
572 more variables requires careful consideration about what values such variables should take
573 when estimating changes in movement behaviour under future conditions.

574 **4.3 Considerations for future work**

575 ***HERE***

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

581 large mammals give clear responses, but they are also already studied most often
582 More work is necessary on quantifying interspecific responses to temperature, including
583 the effects of temperature on predation rates (but see: Cunningham *et al.*, 2021; Glass *et*
584 *al.*, 2021; Brivio *et al.*, 2024). The increase in intensity and frequency of extreme heat events
585 (Bunnell *et al.*, 2011; Yao *et al.*, 2022) will likely also impact the occurrence and timing of
586 hibernation (Wells *et al.*, 2022) and migration or seasonal range expansions (Morley, 2021;
587 Carbeck *et al.*, 2022; Malpeli, 2022). However, not all species may be able to adapt at
588 the current rate of climate change (Heten *et al.*, 2014; Williams & Blois, 2018), especially
589 since landscape changes will likely depend not only on the direct effect of temperature but
590 also on cascading changes in the availability and unpredictability of resources (McLellan &
591 McLellan, 2015; Pigeon *et al.*, 2016; Mezzini *et al.*, 2025).

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

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

604 **Author contributions**

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

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