

Rising temperatures alter how and where boreal 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 how and where these boreal mammals moved, and we predict that climate change will impact mammals' movement behaviour throughout the 21st century. 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 phenology. We also predict that rising temperatures will reduce median habitat selection strength for four of the species, although cougars and elk 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. 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 also determines encounter rates with resources (Mezzini *et al.*, 2025), humans (Johnson
⁸ *et al.*, 2018; Weststrate *et al.*, 2024), predators, prey, and competitors (Martinez-Garcia *et*
⁹ *al.*, 2020; Glass *et al.*, 2021; Brivio *et al.*, 2024). However, ambient temperature affects
¹⁰ animals' movement rates by altering the energetic cost of movement and thermoregulation
¹¹ (McNab, 1970; Taylor *et al.*, 1982; Brown *et al.*, 2004; Fuller *et al.*, 2016; Jahn & Seebacher,
¹² 2022), and extreme temperatures can impact animals' movement rates (Dyer *et al.*, 2023),
¹³ phenology (McLellan & McLellan, 2015; Pigeon *et al.*, 2016; Johnson *et al.*, 2018; Carbeck
¹⁴ *et al.*, 2022), and life history (Newediuk *et al.*, 2024), and even cause physiological damage
¹⁵ and death (Hetem *et al.*, 2014; Powers *et al.*, 2017; Ratnayake *et al.*, 2019; Schmidt *et al.*,
¹⁶ 2020; Schwerdt *et al.*, 2024). Animals may search for a short-term buffer from extreme
¹⁷ temperatures by moving to thermal refugia (Hannah *et al.*, 2014; Elmore *et al.*, 2017; Attias
¹⁸ *et al.*, 2018; Arechavala-Lopez *et al.*, 2019; Gulland *et al.*, 2022), and shelter may even be
¹⁹ preferred over forage abundance (Hall *et al.*, 2016). However, climate change during the last
²⁰ century (IPCC, 2023) has caused animals to alter how and where they move as they respond
²¹ to hotter temperatures and increasingly severe and frequent extreme-heat events (Bunnell
²² *et al.*, 2011; Thompson *et al.*, 2022; IPCC, 2023).

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

27 damage in a shorter span of time (Jessen, 2001; Sherwood & Huber, 2010; Mota-Rojas *et*
28 *al.*, 2021; Newediuk *et al.*, 2024). Mammals' homeothermy can cause them to have difficulty
29 dissipating heat, particularly when ambient temperatures are near or above body tempera-
30 ture. Larger-bodied mammals are more likely to alter their movement behaviour with rising
31 temperatures, since they tend to move long distances (Merkle *et al.*, 2016), are particularly
32 sensitive to overheating (Fuller *et al.*, 2016; Alston *et al.*, 2020; Verzuh *et al.*, 2023), and
33 their movement rates are thus strongly limited by excessive heat (Dyer *et al.*, 2023).

34 Global warming during the last century has resulted in milder and shorter winters, hotter
35 and longer summers, and a greater risk of extreme-heat events (IPCC, 2023), with widespread
36 changes in mammals' phenologies, circadian rhythms, fitness, and life histories (Botero *et*
37 *al.*, 2015; McLellan & McLellan, 2015; Le Corre *et al.*, 2016; Pigeon *et al.*, 2016; Wells *et*
38 *al.*, 2022; Newediuk *et al.*, 2024). However, behavioural responses to heat vary substantially
39 across species depending on body size, vagility, and activity times (McCain & King, 2014;
40 Williams & Blois, 2018). For example, warming temperatures have allowed deer (*Odocoileus*
41 spp.) to shift northward, which has led to increased density of wolves (*Canis lupus*) and
42 higher predation on caribou (*Rangifer tarandus caribou*) (Latham *et al.*, 2011; Barber *et*
43 *al.*, 2018; Dickie *et al.*, 2024). Preparing for and responding to future changes will require
44 a detailed understanding of not only how and where mammals move throughout the
45 thermal landscape but also the cascade of effects that such changes will have at the population
46 and community levels (Cunningham *et al.*, 2021).

47 As heat stress intensifies throughout the 21st century, mammals will continue to suffer
48 impacts on their fitness, movement rates, and habitat selection (Deb *et al.*, 2020; Woo-
49 Durand *et al.*, 2020). It remains unclear how or whether species will be able to respond to
50 climate change in the current century (Deb *et al.*, 2020; Woo-Durand *et al.*, 2020; Verzuh
51 *et al.*, 2023), especially if populations fail to adapt (Botero *et al.*, 2015; Sawyer *et al.*, 2019)
52 or are physiologically incapable to do so (Sherwood & Huber, 2010; Botero *et al.*, 2015;
53 Williams & Blois, 2018). Recent work has documented the effects of climate change on

54 mammals' ranges (Leclerc *et al.*, 2021), thermoregulation (Mota-Rojas *et al.*, 2021), and
55 movement behaviour (McCain, 2019; Cunningham *et al.*, 2021; Melin *et al.*, 2023), but there
56 remains a need for fine-scale estimates of the effects of temperature on mammals' movement
57 behaviour and quantitative predictions of future changes in movement behaviour.

58 In this paper, we quantify the effects of proximal air temperature on mammalian move-
59 ment behaviour, namely movement rates and habitat selection of six large-bodied terrestrial
60 mammal species in western Canada (boreal and southern mountain caribou, cougars: *Puma*
61 *concolor*, elk: *Cervus canadensis*, grizzly bears: *Ursus arctos horribilis*, mountain goats:
62 *Oreamnos americanus*, and wolves; Table 1). Western Canada is currently experiencing
63 accelerating and widespread but spatially heterogeneous warming (Turner & Clifton, 2009;
64 Kienzle, 2018; Dierauer *et al.*, 2021), phenological shifts (plants: Post & Forchhammer, 2008;
65 Tysor, 2025; ice: Basu *et al.*, 2024; caribou: Le Corre *et al.*, 2016), and more frequent and
66 intense extreme heat events (Zhang *et al.*, 2023). Decision makers must understand which
67 areas will best sustain and protect biodiversity not only for current conditions but future
68 decades, too. Failing to understand how climate change will affect mammalian movement
69 behaviour will hinder our ability to respond to the current climate crisis and make deci-
70 sions that are viable in the long term. Furthermore, understanding how temperature affects
71 individual species is the first step towards understanding how temperature impacts the com-
72 munity dynamics (Hegel *et al.*, 2010; Cunningham *et al.*, 2021; Carbeck *et al.*, 2022) and
73 phenology (Bunnell *et al.*, 2011; Duncan *et al.*, 2012; Le Corre *et al.*, 2016; Merkle *et al.*,
74 2016; Slatyer *et al.*, 2022; Gerlich *et al.*, 2025), and how these changes will impact mammals
75 in the coming decades (Sobie *et al.*, 2021; Eum *et al.*, 2023; Weststrate *et al.*, 2024).

Table 1: Summary statistics of each species' set of GPS data, namely: the start and end of each set of GPS telemetry data, the number of GPS fixes (after data cleaning), 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	Fixes	Δt (hours)	Animals	Has speed
Caribou (boreal)	2011-03-02	2018-01-03	200,561	13.00	146	131

Species	Start	End	Fixes	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.

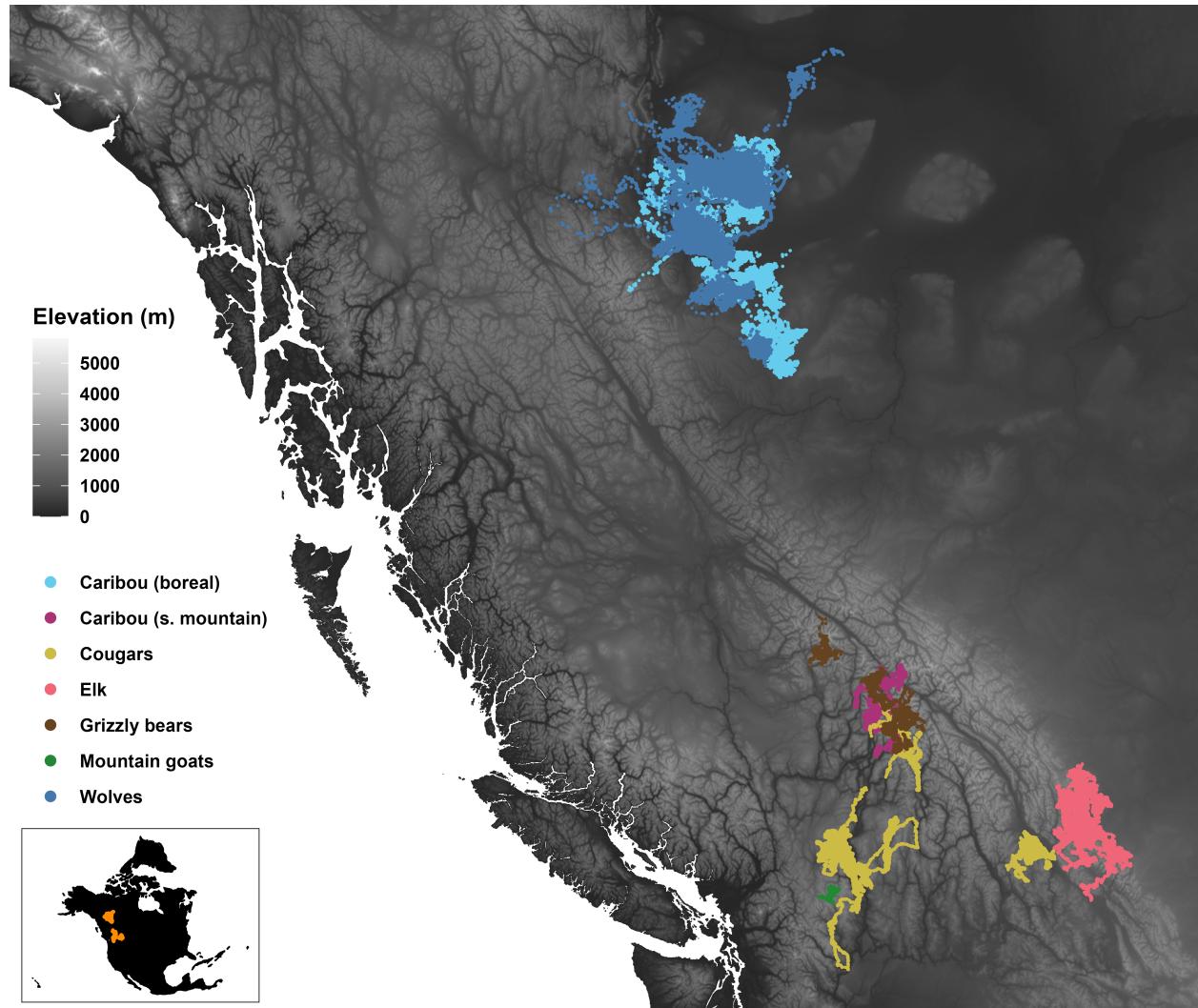


Figure 1: GPS telemetry data for the six species in this study (dots) over a digital elevation model for the study area. The inset in the bottom left shows the telemetry data within the north american continent. Both maps use the BC Albers Equal Area Conic projection (EPSG:3005).

96 **2.1.1 GPS telemetry data**

97 Boreal caribou and wolf telemetry data 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 Effec-
100 tiveness Monitoring Board (REMB; BC OGRIS, 2018). Southern mountain caribou data
101 were obtained from Ford *et al.* (2023). Cougar data are from Darlington *et al.* (2025)
102 and (**serrouya_ref?**). Elk data from the work of Ciuti *et al.* (2012) were downloaded from
103 Movebank (Kays *et al.*, 2022). Finally, grizzly bear telemetry data are from (**grizzly_ref?**),
104 while mountain goat data are from (**goats_ref?**).

105 From the full set of telemetry data, we removed 2,396 problematic GPS locations (0.16%,
106 including collar calibration data) after inspecting diagnostic plots of (1) distance from the
107 median location, (2) straight-line displacement between locations, (3) turning angle, and
108 (4) time interval between consecutive points. Particular attention was paid to points with
109 large turning angles ($\gtrapprox 170^\circ$) and excessively high straight-line displacement, especially if
110 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 To obtain projected average monthly temperatures from 2025 to 2100 at a 0.08° spatial
119 resolution, we used the `climatenetR` package (v. 1.0, Burnett, 2023) for `R` and ClimateNA
120 v. 7.4.2 (Wang *et al.*, 2016; Mahony *et al.*, 2022). However, the climate projections only
121 included estimates of future monthly averages, a scale substantially coarser than that of our

tracking data (Table 1). To estimate the distribution of temperatures at an hourly scale within a month, we assumed values to be approximately normally distributed with mean μ_T and variance σ_T^2 . We estimated μ_T using the ClimateNA projections, while we estimated σ_T^2 by modeling the observed variance in historical weather data for western Canada from 1998 to 2023 (inclusive). For each location $\langle x, y \rangle$ and month m of each year (e.g., the observed variance at coordinates $\langle -119.40, 49.94 \rangle$ in April 2005), we calculated the variance in historical temperature data, for a total of $(2024 - 1998) \times 12 = 312$ observations per location. We then modeled σ_T^2 a Generalized Additive Model (GAM) for Location and Scale (GAMLS, Rigby & Stasinopoulos, 2005; Stasinopoulos & Rigby, 2007; section 7.9 in Wood, 2017) fitted with the `mgcv` package for R (v. 1.9-1, Wood, 2017). The linear predictor 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

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

140 where $\mu_{\sigma_T^2}$ and $\nu_{\sigma_T^2}$ indicate the location and scale parameters of the gamma distribution of
141 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
142 $f_{S,j}$ indicate the j^{th} smooth functions for the location and scale parameters, respectively.
143 To ensure the smooth functions of month, $f_{L,2}(m)$ and $f_{S,2}(m)$, joined smoothly between
144 December and January, the terms use cyclic cubic spline bases. The spatial terms used two-
145 dimensional Duchon splines, a generalization of thin-plate regression splines (p. 221 of Wood
146 (2017)). The smoothness parameters were estimated via REstricted Maximum Likelihood
147 (REML; p. 83 of Wood, 2017). See the Data Availability Statement for additional information
148 on the code used to fit the model.

149 We simulated hourly variation in future years by assuming hourly temperature followed
150 a normal distribution with mean specified by the monthly `climatenar` climate projections
151 and variance as specified by the gamma GMLS. For each month within each year from
152 2025 to 2100, we simulated hourly weather by including temperatures from the 0.1 to the
153 0.9 quantiles by increments of 0.1, and we weighted each quantile proportionally to the
154 normalized Gaussian probability density for each quantile.

155 2.1.3 Habitat rasters

156 We estimated percent forest cover and distance from water using the temporally static
157 rasters created by Tuanmu & Jetz (2014). We calculated total forest cover by summing
158 the four rasters of evergreen/deciduous needle-leaf trees, evergreen broadleaf trees, decidu-
159 ous broadleaf trees, and mixed/other trees (raster classes 1-4, respectively). We converted
160 the raster of percent cover of open water (class 12) to a binary raster of pixels with water
161 (cover $\geq 1\% \approx 40,000\text{m}^2$ for a $\approx 4\text{km}^2$ pixel) or without water (cover $\leq 1\%$) and then
162 calculated each pixel's distance from the nearest pixel with water using the `distance()`
163 function from the `terra` package. We recognize that although this approach may fail to
164 account for small or ephemeral bodies of water, it should still capture large-scale prefer-
165 ences for proximity to water. Finally, we obtained two digital elevation models using the

166 `get_elev_raster()` function from the `elevatr` package (v. 0.99.0, Hollister *et al.*, 2023).
167 We used a raster with a zoom of 6 (a resolution of 0.009°) for model fitting and one with a
168 zoom of 3 (a resolution of 0.08°) for downloading climate change projections via `climatenar`.
169 All final rasters and code are available on GitHub (see the Data Availability Statement). For
170 ease of interpretability and comparison with current conditions, we assumed resources would
171 remain constant through to 2100, although we recognize that the spatial distribution of forest
172 cover and open water will change throughout the 21st century.

173 2.2 Estimating mammals' instantaneous speeds

174 We modeled each animal's movement using continuous-time movement models (Fleming
175 *et al.*, 2014) via the `ctmm` package (v. 1.2.0, Fleming & Calabrese, 2023) for R. We then
176 estimated each mammal's instantaneous speed at each observed location by applying the
177 `ctmm::speeds()` function on all models with finite speed estimates (415 of 433; Fleming *et*
178 *al.*, 2014; Noonan *et al.*, 2019a). The remaining 18 movement models had sampling rates that
179 were too coarse, relative to the animals' directional persistence, to reconstruct the animals'
180 movement trajectories (Noonan *et al.*, 2019a; Nathan *et al.*, 2022; DeNicola *et al.*, 2025).
181 The models were for one mountain goat, 15 boreal caribou, and two southern mountain
182 caribou (Table 1).

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

192 **2.3 Estimating the effects of temperature on mammals' movement behaviour**

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

204 To assess the importance of including temperature as an explicit covariate (as opposed
205 to including its effects with time of day and day of year), we fit models with and without
206 smooth effects of temperature and compared the fits of the two sets of models via analyses
207 of deviance (a form of generalized likelihood ratio tests) following the methods of Section
208 3.3 in Wood (2017). See Appendix B for additional information.

209 **2.3.1 Effects of temperature on movement rates**

210 We estimated the effects of temperature on mammals' instantaneous movement state (mov-
211 ing or not) and speed when moving using two Hierarchical Generalized Additive Models
212 (HGAMs; Pedersen *et al.*, 2019 and Appendix B) with the `mgcv` package for R. The first
213 HGAM estimated the probability that an animal was moving, $P(M)$, with a binomial fam-
214 ily of distributions and logit link function. The second HGAM estimated an animal's speed
215 when moving with a gamma family of distributions and log link function. We fit the models
216 with fast Restricted Maximum Likelihood ('fREML') and discretized covariates (`discrete =`
217 `TRUE`) to optimize computational efficiency with no appreciable losses to model performance

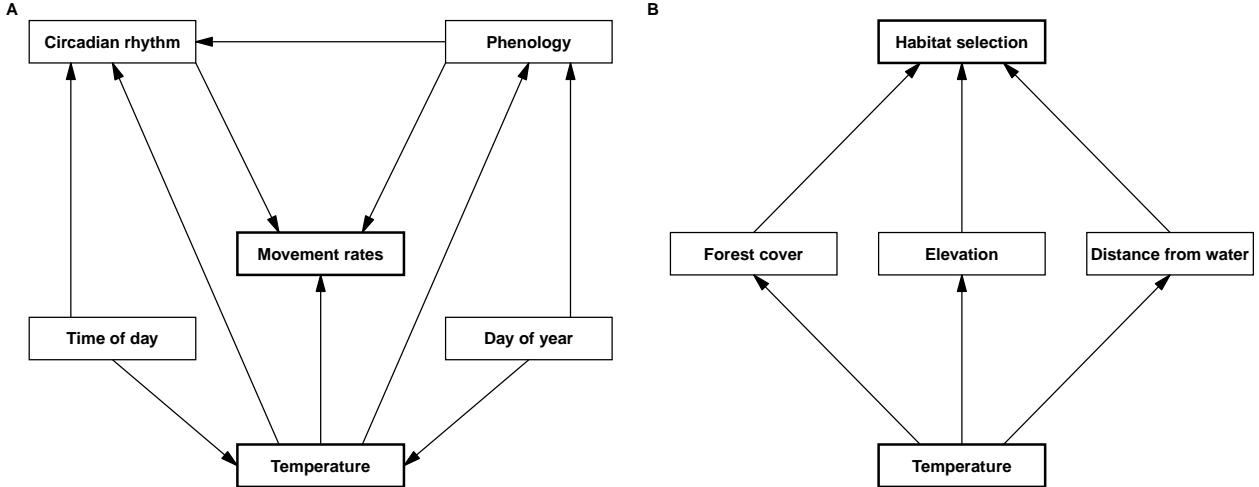


Figure 2: Directed Acyclical Graphs (DAGs) assumed for inferring the causal effects of temperature (red) on each species' movement behaviour. (A) Ambient temperature affects mammals' movement rates (i.e. probability of moving, speed when moving, and their product: hourly distance traveled). The effects of temperature on mammals' movement rates depend on circadian rhythm and phenology, since animals may respond to temperatures differently at different times of day and or days of year. Additionally, temperature varies with time of day and day of year. Finally, circadian rhythm changes with seasonal phenology due to changes in photoperiod (e.g., the time of twilight changes throughout the year, affecting crepuscular activity). (B) Similarly, habitat selection depends on the availability and selection of habitat variables (forest cover, elevation, and distance from water), but the selection strength for each variable is conditional on temperature. For example, an animal may select for more densely-forested areas at extreme temperatures. The resource selection functions for (B) also included marginal smooths of temperature to account for sampling biases across seasons.

218 (Appendix B; Wood *et al.*, 2015, 2017; Li & Wood, 2020). Together, the binomial HGAM
 219 and the gamma HGAM inform us on an animal's long-term average speed, since it is the
 220 product of the probability of moving and its average speed when moving.

221 The HGAMs (equations (2) and (3)) included fixed-effect intercepts for each species
 222 (β_s), random intercepts for each animal (Z_a), and species-level **by** smooths that allowed
 223 independent smoothness parameters for each species (model I in Figure 4 of Pedersen *et*
 224 *al.*, 2019). The **by** smooths accounted for trends in time of day (in Pacific Daylight Time;
 225 `tod_pdt`), day of year (`doy`), and temperature (`temp_c`). To account for the cyclicity of time
 226 of day and day of year, the smooth terms used cyclic cubic splines (p. 202 of Wood, 2017).
 227 The models also had three tensor product interaction terms **by** each species: (1) day of year
 228 and time of day, (2) temperature and time of day, and (3) temperature and day of year.
 229 These three terms accounted for smooth changes in: (1) daily behaviour across day of year,
 230 (2) the response to temperature over time of day (e.g., changes in nocturnality), and (3)

231 the response to temperature over day of year (e.g., the timing of molting, migration, and
 232 hibernation). Finally, two smooth terms of log-transformed sampling interval (dt ; hours)
 233 corrected for biases in speed estimates arising from irregular GPS sampling intervals, since
 234 longer intervals result in lower speed estimates (Nathan *et al.*, 2022; DeNicola *et al.*, 2025).
 235 A global smooth term of $\log(\text{dt})$ accounted for the overall effect of sampling interval, while
 236 a factor-smooth interaction term ($\text{bs} = \text{'fs'}$) of $\log(\text{dt})$ and species accounted for species-
 237 level deviations from the global term while assuming a common smoothness parameter across
 238 species (model GS in Figure 4 of Pedersen *et al.*, 2019). Formally, the model for movement
 239 state M , with $M = 0$ indicating no movement and $M = 1$ indicating movement, was

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

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

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

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

245 **2.3.2 Effects of temperature on habitat selection**

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

261 Each species' model had the same structure:

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

where O indicates whether an animal was observed ($O = 1$) or not ($O = 0$), and the species-level indices are omitted for readability, but each term in the model can be assumed to be species-specific. Smooth effects of percent forest cover (`forest_perc`), elevation (`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). 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). 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 overall speed (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 hourly 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 of $T = 0^{\circ}\text{C}$.

Species	n	T< -20°C (%)	T> $+20^{\circ}\text{C}$ (%)	$\hat{P}(M = 1 T)$	$\hat{\mathbb{E}}(S M = 1, T)$	$\hat{\mathbb{E}}(D T)$
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			

Across all species, Relative Selection Strength (RSS) was weakest for forest cover and strongest for elevation. At temperatures near 0°C, boreal caribou selected for forest cover

293 between 50% and 75%, elevations near 500 m, and distances from water < 10 km, while
294 southern mountain caribou selected for dense forest cover, elevations near 2 km, and distances
295 from water \lesssim 5 km. Cougars selected for dense forest cover ($> 75\%$), an elevation of ~ 1
296 km, and distances from water < 7.5 km. Elk selected for intermediate forest cover ($\approx 50\%$),
297 elevations between 1 and 2 km, and distances from water of 10-15 km. Grizzly bears selected
298 for relatively sparse forest cover (25-50%), elevation between 1 and 2 km, and distances from
299 water < 3 km. Mountain goats selected for sparse forest cover (< 25%), elevations near
300 1.5 km, and distances from water < 5 km. Finally, wolves selected for forest cover (\gtrapprox
301 50%), elevations near 1 km, and distances from water < 5 km. There was relatively strong
302 agreement between models with and without temperature (Figs. B3, and B14), but including
303 temperature always resulted in better fits (all p-values $< 2.2 \times 10^{-16}$; all $\Delta AIC \geq 342$;
304 Appendix B). Accounting for temperature even resulted in a simpler HRSF for mountain
305 goats (lower model degrees of freedom due to simpler random smooth terms) that fit the
306 data better (lower deviance), and hence no test was necessary to show that the inclusion of
307 temperature produced a better fit.

308 3.1 Effects of temperature on movement rates

309 Species' changes in movement rates to temperature varied in both direction and magnitude
310 (Figs. 3, B4-B6), even after accounting for differences in daily and seasonal activity (e.g.,
311 sleeping, migration, hibernation; Figs. B4-B6). Smooth interaction terms were well-behaved
312 and indicated clear shifts in activity over time of day and day of year for all species. The
313 models had good in-sample prediction (Fig. B7) and explained reasonably high proportions
314 of the deviance [79.3% for the gamma model and 10.7% for the binomial model, which is
315 relatively high for a binomial model with binary responses]. All species altered their daily
316 and seasonal movement behaviour to changes in temperature (Fig. 3). The response was
317 most visible in cougars. In late spring (June 1st), they moved from evening to early morning
318 if hourly 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. Overall, uncertainty around the estimated effects was generally higher at extreme temperatures due to lower data availability (Figs. B4A, B5A, and B6A).

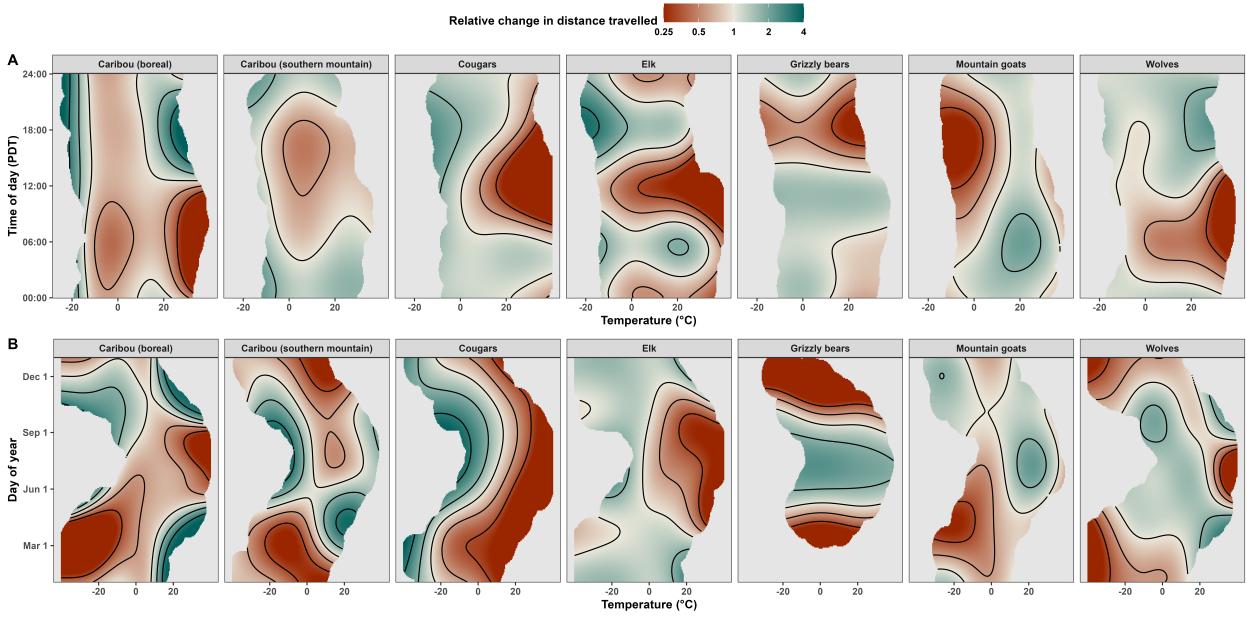


Figure 3: **Temperature is a strong driver of how far and when mammals travel.** The fill indicates the effects of temperature on the relative change in hourly distance travelled (probability of moving times mean speed when moving) over time of day on June 1st (**A**) and day of year at 12:00 PDT (**B**).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

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 except cougars exhibited clear temperature-dependent shifts in their preference for forest cover. At higher temperatures, wolves relaxed their preference for forested areas, while mountain goats relaxed their preference for 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, but species varied in the magnitude, direction, and complexity of their responses. As temperatures warmed, elk, mountain goats, and cougars moved to higher elevations, while wolves, southern mountain caribou, and grizzly bears moved to lower elevations. Cougars' selection for higher elevation strengthened substantially at temperatures $\gtrapprox 20^{\circ}\text{C}$, while mountain goats and wolves showed strong switches in preferences near 10°C . 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 were scarcer (Fig. B15).

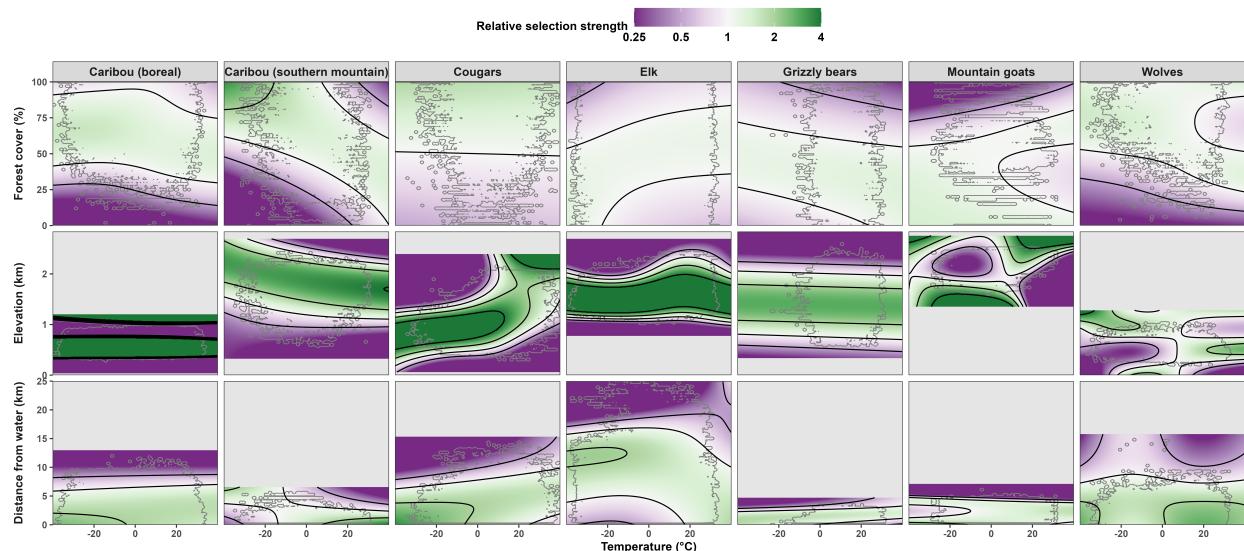


Figure 4: Mammals' habitat selection depends on ambient temperature. Estimated relative selection strength (RSS) for forest cover (%), elevation (km), and distance from water (km) as a function of temperature. The grey contours indicate the extent of each species' observed data. RSS values were re-centered and capped between 0.25 and 4 ($2^{\pm 2}$) to improve readability.

Fig. 5 presents the predicted habitat selection for boreal caribou and wolves. Overall, both species selected for the same low-elevation area (< 500 m; Fig. 5A-B), but caribou generally avoided the river system that wolves were often found at, and their selection strength varied with temperature. As wolves' habitat selection strengthened at warmer temperatures, co-occupancy at 20°C was approximately four times more likely than at -

348 20°C, independent of changes in the species' movement rates (Fig. 5C).

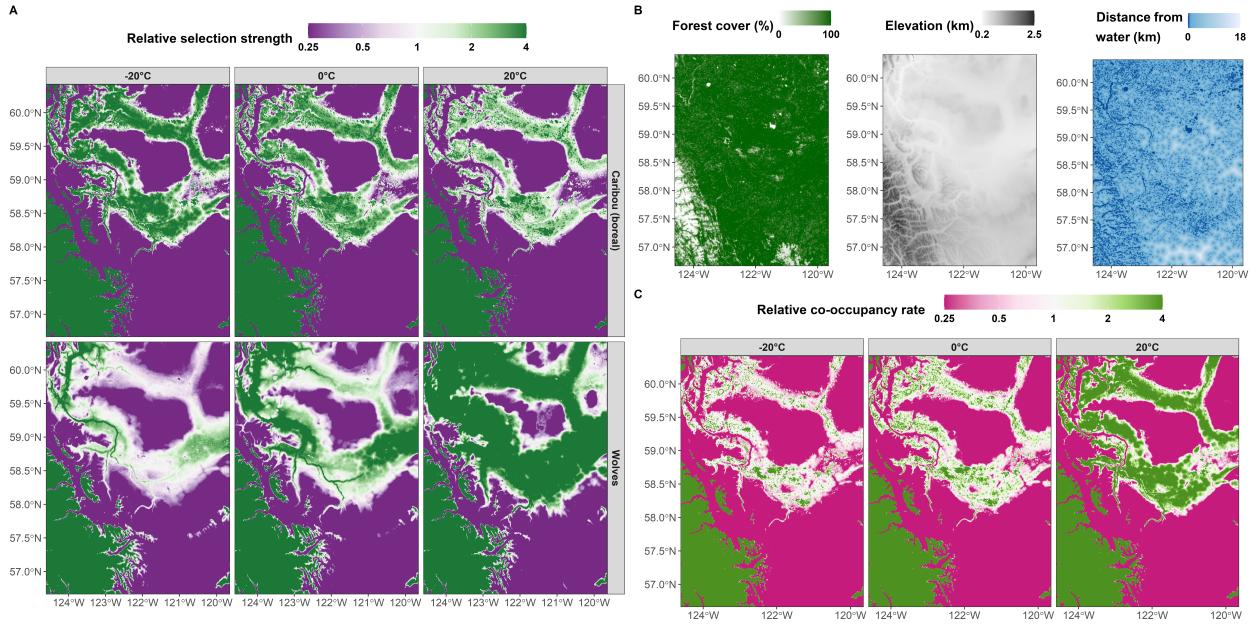


Figure 5: **Temperature affects boreal caribou's and wolves' habitat selection and, consequently, their encounter rates.** Panel (A) shows the rasters of the three habitat variables used in the hierarchical resource selection functions, while panel (B) shows the relative selection strength (RSS) for boreal caribou and wolves, as a function of temperature. RSS values were re-centered and capped to between 0.25 and 4 ($2^{\pm 2}$) to improve readability. Finally, panel (C) shows the (scaled) product of the RSS values in panel (B) as a proxy for the co-occupancy of the two species.

349 3.3 Predicted changes in movement behaviour during the 21st century

350 Predicted changes in movement rates with future climate change varied across species in both
 351 magnitude and direction, but worse SSPs always corresponded to greater absolute changes
 352 (Fig. 6). Additionally, species that were predicted to move less often did not necessarily
 353 have lower speeds when moving, and vice versa (Figs. B9 and B10). Estimated changes in
 354 average yearly distance traveled were negligible for boreal caribou and grizzly bears, although
 355 both species showed seasonal changes in seasonal movement rates. As temperatures warmed,
 356 boreal caribou were predicted to move more in winter, spring, and fall but less in summer
 357 (Fig. 3), while grizzly bears were predicted to show a clear shift towards earlier emergence
 358 from hibernation (Fig. B4) and greater movement earlier in the year but less movement in
 359 early fall. Southern mountain caribou and mountain goats are projected to travel further by
 360 2100, although the estimates for southern mountain caribou varied greatly over space (Fig.

361 7). Cougars, elk, and wolves were projected to move less by 2100, with cougars showing as
 362 much as a 24% decrease in mean yearly distance travelled.

363 Absolute relative changes in predicted yearly distance travelled were small under the
 364 best-case SSP (0-4% change in 2100 relative to 2025). Under the worst-case SSP, absolute
 365 changes by 2100 (relative to 2025) ranged from ~2% (grizzly bears) to ~24% (cougars).
 366 Projected changes in 2100 varied spatially due to spatial heterogeneity in climate change
 367 projections (Fig. 7). Again, absolute changes were generally greatest under worse SSPs, but
 368 the direction of change at each location also varied across SSPs (most visible in cougars).

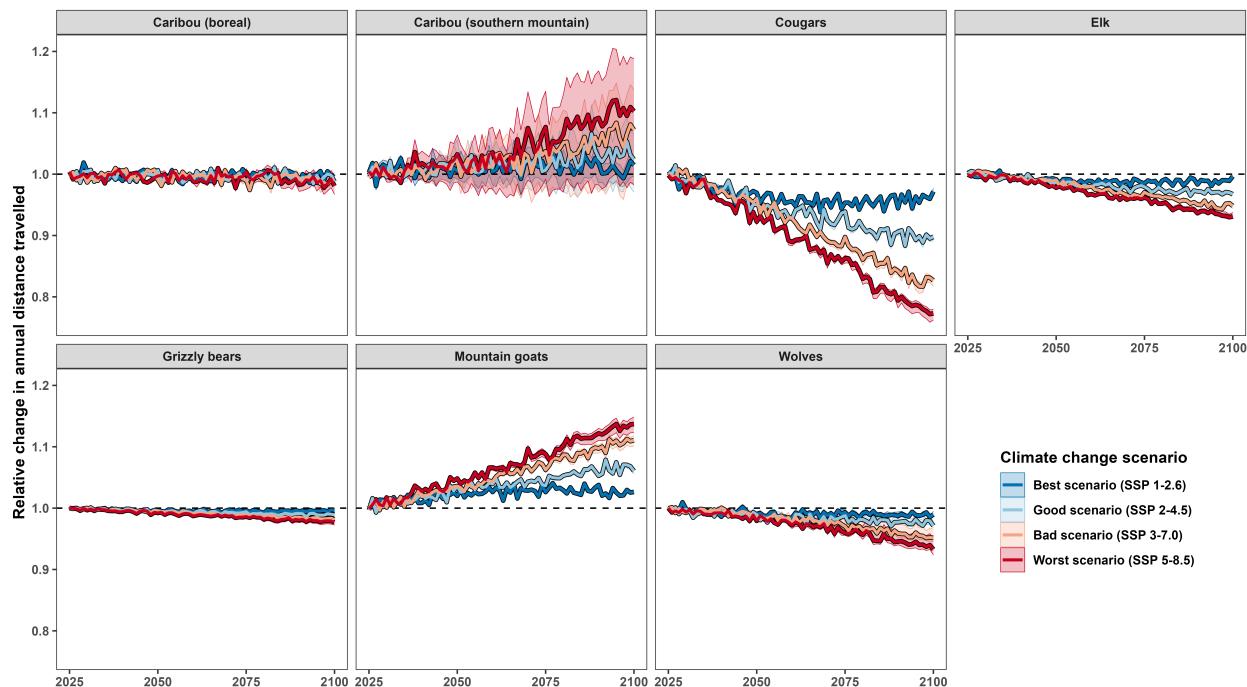


Figure 6: Species are predicted to alter their movement rates differently in response to climate change, and worse climate-change scenarios will result in the greatest change. Bold lines indicate the median change in yearly distance travelled (probability of moving times speed when moving) due to predicted changes in temperature within each species' study area. 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.

369 Median RSS was projected to decrease over time within each species' observed range, but,
 370 again, changes were stronger under worse SSPs (Fig. 8). Decreases were most pronounced
 371 in areas with the lowest RSS and most severe for elk, mountain goats, cougars, and southern
 372 mountain caribou. Changes for boreal wolves and caribou were negligible. Elk, cougars,

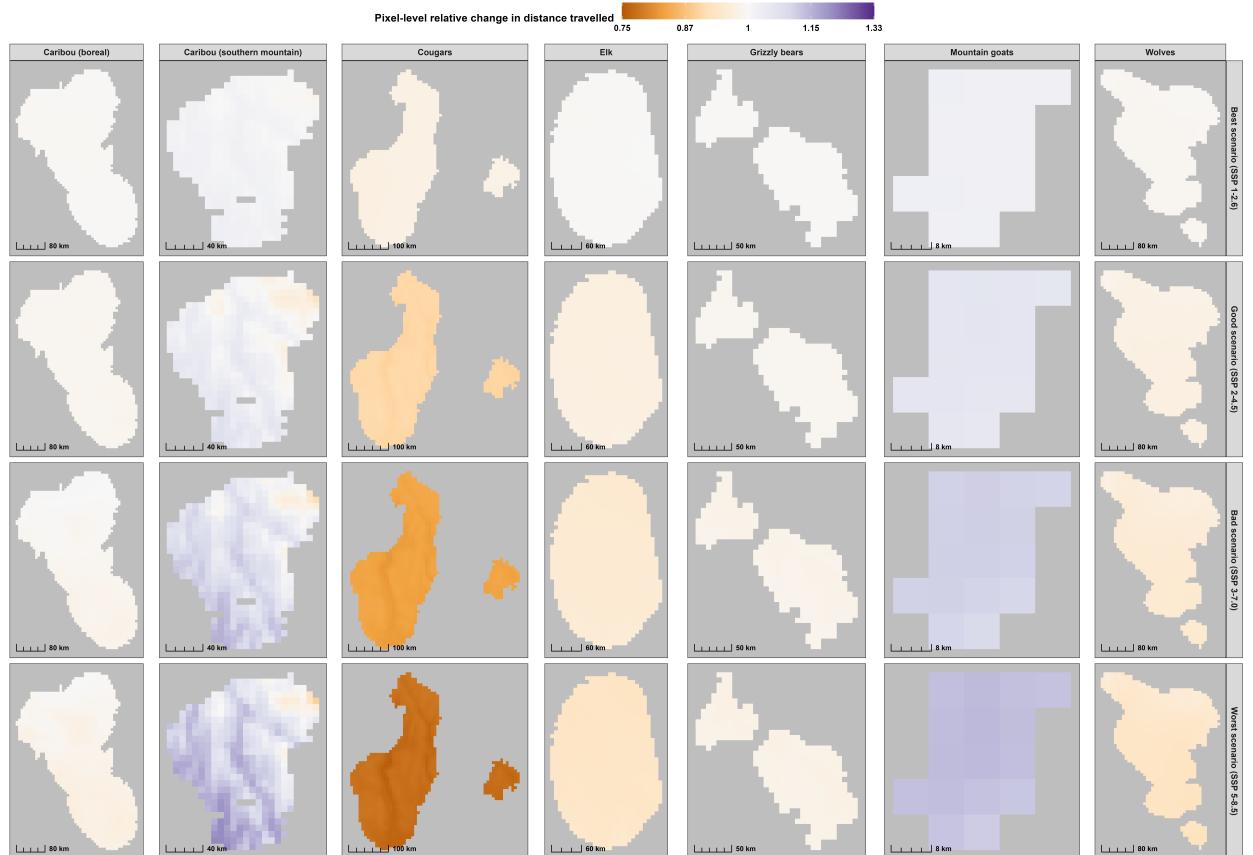


Figure 7: Climate change is predicted to impact each species' movement rates differently, but changes will also vary spatially. The color of each pixel indicates the predicted changes in distance traveled in 2100 at that pixel, relative to the value in 2025, averaged across all four scenarios. Values < 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 cover. All maps extend to each species' study area (Fig. 1) and are shown in the BC Albers Equal Area Conic projection (EPSG:3005).

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 predicted change in RSS between 2025 and 2100 also varied spatially for all species (Fig. 9). 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 the species were projected to increase RSS throughout their habitat (10).

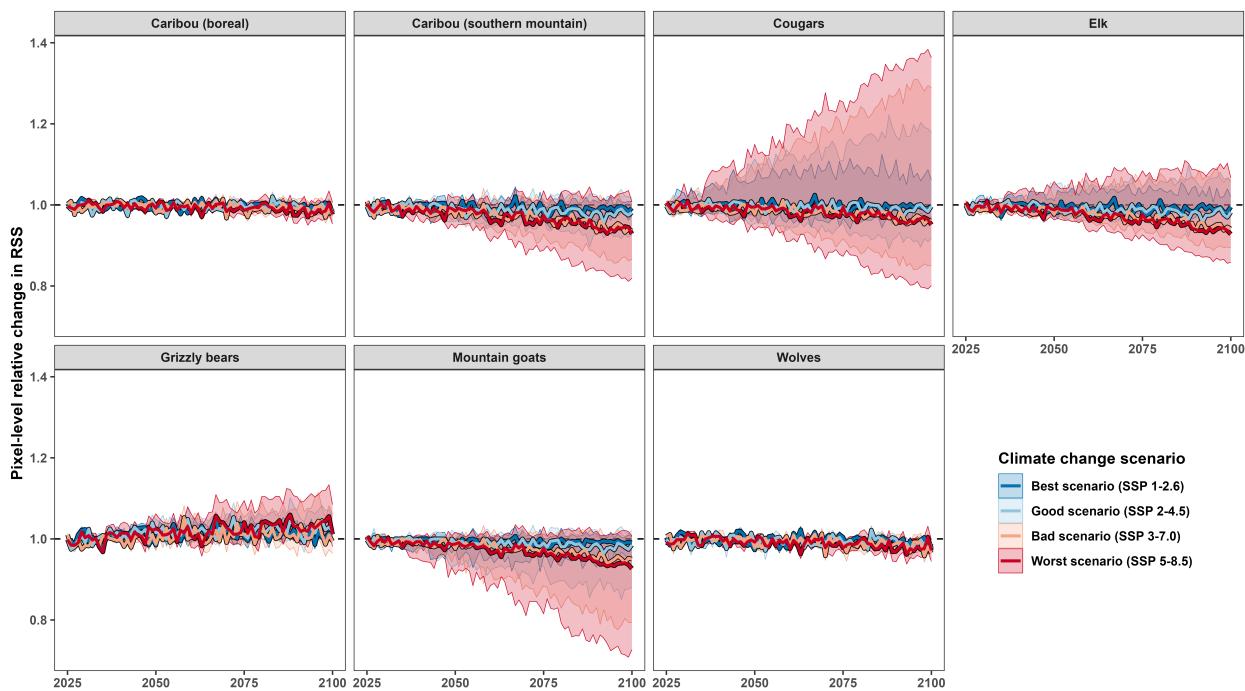


Figure 8: Species are predicted to alter their habitat selection differently in response to climate change, and worse climate-change scenarios will result in the greatest change. Bold lines indicate the change in median RSS due to predicted changes in temperature within each species' study area. Shaded 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).

4 Discussion

We have demonstrated that temperature is an important driver of how and where large boreal mammals move, and that it affects mammals' seasonal and daily movement behaviour in complex and nonlinear ways. However, predicting mammals' responses to climate change



Figure 9: 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' study area and are shown in the BC Albers Equal Area Conic projection (EPSG:3005).

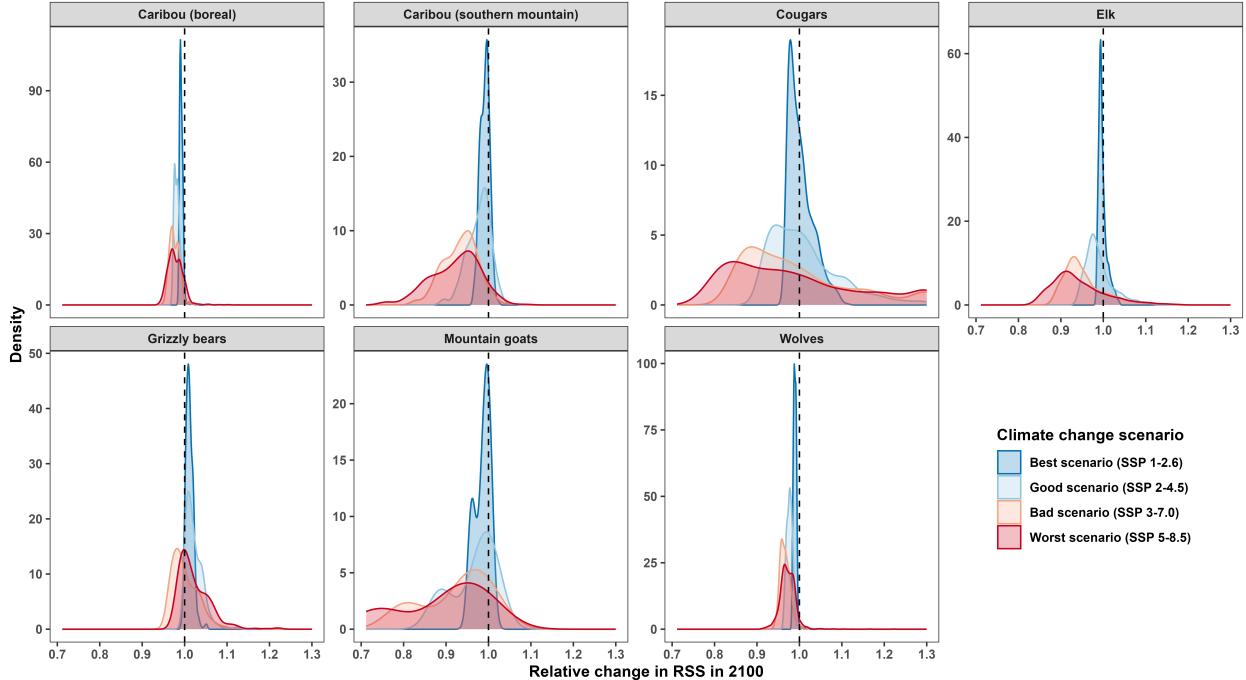


Figure 10: Climate change is predicted to cause species to decrease their selection strength for their current habitats, and worse climate change scenarios will have the greatest impact. The density plots indicate each species’ change in RSS in 2100 for their current habitat (Fig. 8), relative to each 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).

remains a challenge, as habitats are warming rapidly and mammals are exposed to increasingly novel and extreme conditions (Diffenbaugh & Field, 2013; Botero *et al.*, 2015; IPCC, 2023). We leveraged the flexibility and interpretability of HGAMs to estimate mammals’ nonlinear responses to temperature without imposing rigid assumptions about the shape of the responses (Simpson, 2018, 2025). In particular, tensor product interaction terms were crucial for estimating smooth, nonlinear changes in daily and seasonal trends with temperature with data from multiple individuals. By allowing interaction terms to be smooth bivariate functions, we were able to quantify changes in movement behaviour without the need to discretize time into windows (e.g., day/night and seasons). We were thus able to present results using relatively simple and interpretable surface plots (Figs. 3 and 4) that conveyed nuanced, continuous-time estimates of change. This framework was essential for estimating how mammals behave at extreme temperatures. In fact, despite the recent increase in frequency of extreme heat events in western Canada, including a severe heat wave

397 in 2021 (Kienzle, 2018; Thompson *et al.*, 2022; Zhang *et al.*, 2023), such events remain rela-
398 tively rare, so estimating mammals' nonlinear responses required the flexibility provided by
399 HGAMs (Wood, 2017). Additionally, the hierarchical approach allowed us to leverage data
400 from multiple individuals in a single model while accounting for differences in behaviour and
401 data availability across individuals (Pedersen *et al.*, 2019; Muff *et al.*, 2020; McCabe *et al.*,
402 2021; Jeltsch *et al.*, 2025; Silva *et al.*, 2025). Still, GAMs' flexibility and complexity can be a
403 frustrating limitation if used too generously, so we suggest choosing each smooth term's basis
404 size (k) carefully and confirming that estimated responses align with the species' ecology.
405 While penalized splines and REML can help avoid unruly smooth terms, the penalty terms
406 can struggle to restrict model complexity when datasets are as large as those presented here
407 (Wood, 2017; Wood *et al.*, 2017), so estimated responses should be aligned with biological
408 relevance rather than statistical significance.

409 The effects of warming temperatures on movement rates varied across species, seasons,
410 and space due to differences in species' behavior and physiology as well as their habitats'
411 phenology (e.g., the timing of green-up). For boreal caribou, hotter temperatures decreased
412 movement rates summer but increased them otherwise, mirroring previous studies (Stien *et*
413 *al.*, 2012; Leclerc *et al.*, 2021; Lessard *et al.*, 2025). The increase in movement rates with
414 temperature during the cold months is likely partly due to shallower snow depth, which
415 results in greater mobility (Pedersen *et al.*, 2021), but warmer temperatures during snowy
416 seasons also increase the risk of rain-on-snow events, which limit forage availability and
417 increase time spent foraging (Stien *et al.*, 2012; Berger *et al.*, 2018; Mezzini *et al.*, 2025).
418 The reduced movement rates during warmer summers are likely mainly due to more frequent
419 resting and use of thermal refugia, given ungulates' documented risk of hyperthermia (Alston
420 *et al.*, 2020; Verzuh *et al.*, 2023). Therefore, although we predict that boreal caribou's
421 yearly average movement rates will remain approximately unchanged throughout the 21st
422 century, the projections do not show the changes in seasonal movement phenology. This is an
423 important caveat, since the effects of extreme temperatures are exacerbated by phenological

424 mismatches with seasonal photoperiod (Walker *et al.*, 2019), including the timing of molting
425 and reproduction. Earlier growth seasons in boreal and arctic regions have resulted in lower
426 calf birth and survival (Post & Forchhammer, 2008), while the lengthening of the growth
427 season has allowed moose (*Alces alces*) and deer to encroach on boreal caribou habitat and
428 increase the density of coyotes (*Canis latrans*), cougars, and wolves (Barber *et al.*, 2018;
429 DeMars *et al.*, 2023), whose movement behaviour also depends on ambient temperature.

430 Boreal wolves responded to temperature similarly to boreal caribou, and habitat selection
431 strength was not projected to change noticeably by 2100, but wolves were predicted to move
432 less in future decades. In contrast, cougars showed markedly different seasonal responses
433 to temperature, with warmer temperatures always resulting in less travel, which resulted
434 in strong predicted decreases in movement rates over the 21st century. However, spatial
435 heterogeneity in habitat, climate, and cougar behaviour may cause boreal individuals to
436 respond to temperature differently from those in our study. Still, rising temperatures clearly
437 affect more than each individual species' movement behaviour; they have complex effects
438 on entire communities and their trophic structures. Cunningham *et al.* (2021) discuss the
439 importance of adopting a community-level perspective when assessing the effects of climate
440 change on animals' movement behaviour and phenology. For example, as temperatures
441 warm and both boreal caribou and wolves increase their movement rates in fall, winter, and
442 spring, they also increase their encounter rates (Martinez-Garcia *et al.*, 2020), which will
443 likely increase predation risk when caribou are pregnant or with young calves. Additionally,
444 while both species saw reduced movement rates during hot summer days, boreal wolves' use
445 of anthropogenic linear features (e.g., roads, seismic lines) may allow them to reduce the
446 total thermal costs of movement by moving for shorter periods while increasing the chances
447 of encountering heat-stressed prey (Whittington *et al.*, 2011; Dickie *et al.*, 2017; Dickie *et al.*,
448 2022). Furthermore, caribou that attempt to reduce predation risk from wolves by avoiding
449 wolf habitat may still risk increasing predation pressure from bears, cougars, and coyote
450 (Leblond *et al.*, 2016; DeMars *et al.*, 2023; Labadie *et al.*, 2023).

451 Considerations about changes in trophic interactions leads to another important caveat
452 about the results we present. The estimated changes in movement behaviour cannot be fully
453 attributed to physiological responses to temperature alone, since other aspects of habitats'
454 seasonal phenology are (nonlinearly) correlated with temperature. For example, mountain
455 goats' lower movement rates at temperatures near 0°C in winter may be in part due to
456 increased movement difficulty, since melting snow and rain-on-snow events increase the en-
457 ergetic costs of movement (White, 2025) and encounter rates with predators (Sullender *et*
458 *al.*, 2023). However, milder temperatures can also increase plant growth, which allows goats
459 to spend more time foraging within and less time travelling across patches (Charnov, 1976;
460 White *et al.*, 2025). Therefore, figure 3 illustrates an estimate of the total effects of temper-
461 ature on each species' movement rates, but it does not explicitly account for energetic costs.
462 Similarly, species' changes in habitat selection do not explicitly account for any changes in
463 physiological or energetic costs. Additionally, forest cover, elevation, and distance from water
464 are often correlated, so the estimated effects should be interpreted carefully, and they may
465 not be applicable outside the study areas used here. For example, both mountain goats and
466 elk selected for higher elevation as temperatures warmed, but our models did not account
467 for differences in forage availability at different elevations.

468 Climate change has also had extensive impacts on plant growth and phenology (Cleland *et*
469 *al.*, 2007; Denny, 2019; Tysor, 2025) with consequences on herbivores' behaviour and fitness
470 (Post & Forchhammer, 2008; Aikens *et al.*, 2017). Additionally, plants' limited ability to
471 disperse to and establish in new habitats is often a limiting factor for herbivores' ability to
472 escape hotter temperatures by moving to higher altitudes or latitudes, and the advance of
473 herbivores can further limit plants' ability to establish (Speed *et al.*, 2012; Diffenbaugh &
474 Field, 2013). Consequently, mammals that move to higher elevations may be forced to spend
475 more time foraging (Mezzini *et al.*, 2025), which will increase both their energetic expenditure
476 and encounter rates with predators and competitors (Kohl *et al.*, 2019; Martinez-Garcia *et*
477 *al.*, 2020; Tórrez-Herrera *et al.*, 2020; Smith *et al.*, 2023). If local peaks become unsuitable

478 habitat, and moving to nearby higher peaks requires traveling across low-quality and high-
479 risk habitat (Figure 9), habitat fragmentation may prevent movement across ranges (White
480 *et al.*, 2025).

481 Growing evidence suggests that mammals' exposure, sensitivity, and adaptability to cli-
482 mate change will limit their ability to adapt to change (Ameca y Juárez *et al.*, 2012; Diffen-
483 baugh & Field, 2013). Exposure to warming temperatures is widespread throughout western
484 Canada (Bunnell *et al.*, 2011; Kienzle, 2018; Eum *et al.*, 2023), and changes in temperature
485 and phenology may be too rapid for many species to respond to (Diffenbaugh & Field, 2013).
486 Species' adaptability is further challenged by the difficulty in responding to concurrent, mul-
487 tifarious, and interconnected changes (Diffenbaugh & Field, 2013; Polazzo *et al.*, 2024). In
488 the future, landscapes may thus become unable to support species and population sizes they
489 supported historically, and species may begin selecting against historical ranges (Williams
490 & Blois, 2018). Therefore, it is crucial for conservationists to distinguish between a species'
491 ideal environmental space and its best available geographic space (*sensu* Matthiopoulos,
492 2022).

493 Accelerating multifarious change in species' movement behaviour and energetic costs re-
494 quire conservation measures that are proactive and anticipate future changes. Polazzo *et al.*
495 (2024) present a framework for estimating species' responses to multifarious change using
496 GAMs that is particularly useful when estimating species' (nonlinear) responses to inter-
497 actions between environmental variables (e.g., changes in both temperature and limiting
498 nutrients). By accounting for the effects of multiple variables at once, they demonstrate
499 how a species' response to one variable can depend on other concurrent changes. Estimat-
500 ing responses to multifarious change is crucial in assessing mammals' responses to hotter
501 temperatures, altered phenology, and novel community dynamics.

502 Protected areas must support populations not only in present conditions but also as
503 species' needs and behaviour change over the decades (Simmons *et al.*, 2021; Livingstone *et*
504 *al.*, 2023). Recent evidence has questioned whether current protected areas will be effective

505 in the long term (Loarie *et al.*, 2009; Diffenbaugh & Field, 2013; Williams & Blois, 2018),
506 and increasingly more experts have been calling for proactive and long-term conservation.
507 By identifying and actively protecting climate change refugia and corridors, we may be able
508 to reduce the effects of climate change on mammalian movement behaviour and community-
509 level responses and ensure that protected areas may be viable for decades to come (Michalak
510 *et al.*, 2018; Graham *et al.*, 2019; Stralberg *et al.*, 2020; Hua *et al.*, 2022).

511 Future work should develop models that account for covariates that are specific to the
512 study species and area, such as forest age and disturbance (DeMars *et al.*, 2023), terrain
513 ruggedness (White & Gregovich, 2017), anthropogenic linear features (Dickie *et al.*, 2017),
514 and growing human presence in wild spaces (Sih *et al.*, 2011; Rice, 2022), including the
515 growing risk of human-wildlife conflict (Abrahms *et al.*, 2023; Weststrate *et al.*, 2024). In
516 particular, forests in western Canada are highly dynamic over time (Zhang *et al.*, 2015), and
517 fires size and burn severity have increased in western Canada in recent decades (Whitman *et*
518 *al.*, 2022; Parisien *et al.*, 2023; Wang *et al.*, 2025). Thus, while our use of a static raster of
519 forest cover allowed for simpler models and climate change projections, future studies should
520 account for mammals' responses to temporal forest dynamics, including the impacts of fire
521 (Whitman *et al.*, 2022; Parisien *et al.*, 2023; Wang *et al.*, 2025), logging (Lochhead *et al.*,
522 2022) and other extractive industries (Dickie *et al.*, 2017, 2024). However, the inclusion of
523 temporally dynamic variables will require that any future projections of species' behaviour
524 depend on temporally dynamic estimates of how such variables will change over time with
525 changes in climate and anthropogenic activity.

526 We have demonstrated that temperature has complex and nonlinear effects on how and
527 where boreal mammals move. Rising temperatures have impacted mammals' daily and sea-
528 sonal movement cycles, and changes are expected to intensify throughout the 21st century.
529 Quantifying how temperature affects mammalian behavior and fitness is a first step towards
530 developing an understanding of the effects of climate change on landscape dynamics and the
531 effectiveness of protected areas in the future. By leveraging the flexibility and statistical

532 power of Hierarchical Generalized Additive Models, we have provided researchers with mal-
533 leable and data-driven methods for assessing species' responses to climate change. We hope
534 that future work will develop more species-specific models with the intent of developing a
535 community-level framework for quantifying and predicting how communities will respond to
536 climate change.

537 **Author contributions**

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

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