

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), and predators, prey, and competitors (Martinez-Garcia
⁹ *et al.*, 2020; Glass *et al.*, 2021; Brivio *et al.*, 2024), including infected and parasitized indi-
¹⁰ viduals (Blanchong *et al.*, 2018). However, ambient temperature affects animals' movement
¹¹ rates by altering the energetic cost of movement and thermoregulation (McNab, 1970; Taylor
¹² *et al.*, 1982; Brown *et al.*, 2004; Fuller *et al.*, 2016; Jahn & Seebacher, 2022), and extreme
¹³ temperatures can impact animals' movement rates (Dyer *et al.*, 2023), phenology (McLellan
¹⁴ & McLellan, 2015; Pigeon *et al.*, 2016; Johnson *et al.*, 2018; Carbeck *et al.*, 2022), and life
¹⁵ history (Newediuk *et al.*, 2024), and even cause physiological damage and death (Heten
¹⁶ *et al.*, 2014; Powers *et al.*, 2017; Ratnayake *et al.*, 2019; Schmidt *et al.*, 2020; Schwerdt
¹⁷ *et al.*, 2024). Animals may search for a short-term buffer from extreme temperatures by
¹⁸ moving to thermal refugia (Hannah *et al.*, 2014; Elmore *et al.*, 2017; Attias *et al.*, 2018;
¹⁹ Arechavala-Lopez *et al.*, 2019; Gulland *et al.*, 2022), and shelter may even be preferred
²⁰ over forage abundance (Hall *et al.*, 2016). However, climate change during the last century
²¹ (IPCC, 2023) has caused animals to alter how and where they move as they respond to
²² hotter temperatures and increasingly severe and frequent extreme-heat events (Bunnell *et*
²³ *al.*, 2011; Thompson *et al.*, 2022; IPCC, 2023).

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

et al., 2020; Glass *et al.*, 2021), extreme heat can often result in more severe physiological 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. Larger-bodied mammals are more 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' phenologies, circadian rhythms, fitness, and life histories (Botero *et al.*, 2015; McLellan & McLellan, 2015; Le Corre *et al.*, 2016; Pigeon *et al.*, 2016; Wells *et al.*, 2022; Newediuk *et al.*, 2024). However, behavioural 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 deer (*Odocoileus* spp.) 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 and where mammals move throughout the thermal landscape 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 throughout the 21st century, 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;

54 Williams & Blois, 2018). Recent work has documented the effects of climate change on
55 mammals' ranges (Leclerc *et al.*, 2021), thermoregulation (Mota-Rojas *et al.*, 2021), and
56 movement behaviour (McCain, 2019; Cunningham *et al.*, 2021; Melin *et al.*, 2023), but there
57 remains a need for fine-scale estimates of the effects of temperature on mammals' movement
58 behaviour and quantitative predictions of future changes in movement behaviour.

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

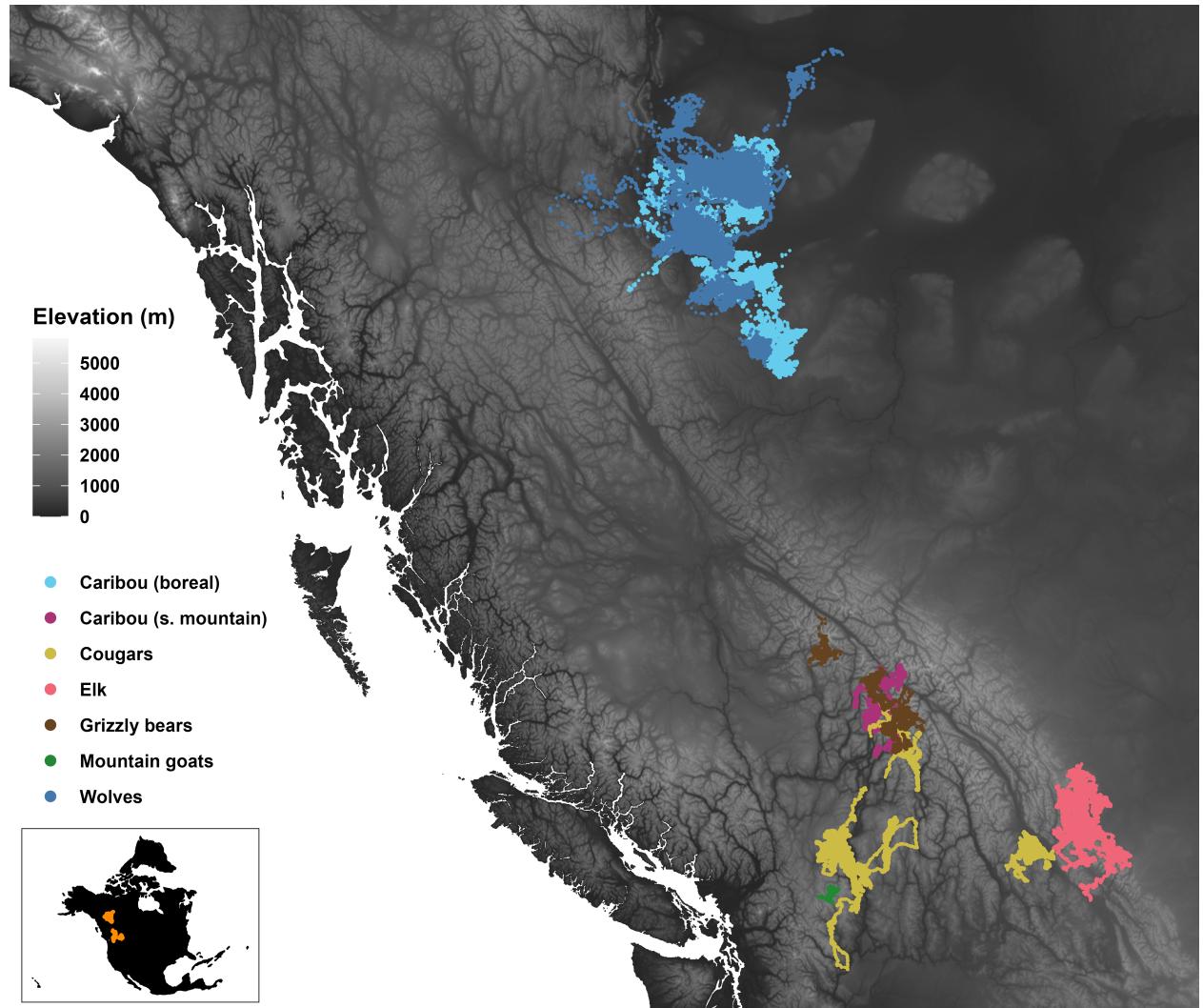


Figure 1: GPS telemetry data for the six species in this study (dots) over a digital elevation model for the study area. The inset in the bottom left shows the telemetry data within the north american continent. Both maps use the BC Albers Equal Area Conic projection (EPSG:3005).

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
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

77 2 Methods

78 2.1 Datasets used

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

92 We acknowledge that our models of habitat selection ignore many important variables of

93 habitat selection (e.g., forest type, structure, and age; terrain slope and aspect; prey avail-
94 ability; population density). We limited our models to only use three simple and temporally
95 static rasters to produce simple and easily interpretable estimates and forecasts under the
96 assumption of temporally invariant landscapes.

97 2.1.1 GPS telemetry data

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

107 From the full set of telemetry data, we removed 2,396 problematic GPS locations (0.16%,
108 including collar calibration data) after inspecting diagnostic plots of (1) distance from the
109 median location, (2) straight-line displacement between locations, (3) turning angle, and
110 (4) time interval between consecutive points. Particular attention was paid to points with
111 large turning angles ($\gtrapprox 170^\circ$) and excessively high straight-line displacement, especially if
112 antecedent and subsequent points indicated relatively stationary behaviour (Appendix A).

113 2.1.2 Historical temperature data and climate change projections

114 Rasters of hourly air temperature data were downloaded from the ERA5 database (Hers-
115 bach *et al.*, 2023) from the European Center for Medium-range Weather Forecasting server
116 (ECMWF; www.ecmwf.int; <https://cds.climate.copernicus.eu>). Proximal air temperature
117 was estimated for each location by extracting the value from the corresponding raster cell

118 from the temporally nearest raster using the `extract()` function from the `terra` package
119 (v. 1.7-46, Hijmans, 2023) for `R` (R Core Team, 2024).

120 To obtain projected average monthly temperatures from 2025 to 2100 at a 0.08° spatial
121 resolution, we used the the `climatenetR` package (v. 1.0, Burnett, 2023) for `R` and ClimateNA
122 v. 7.4.2 (Wang *et al.*, 2016; Mahony *et al.*, 2022). However, the climate projections only
123 included estimates of future monthly averages, a scale substantially coarser than that of our
124 tracking data (Table 1). To estimate the distribution of temperatures at an hourly scale
125 within a month, we assumed values to be approximately normally distributed with mean μ_T
126 and variance σ_T^2 . We estimated μ_T using the ClimateNA projections, while we estimated
127 σ_T^2 by modeling the observed variance in historical weather data for western Canada from
128 1998 to 2023 (inclusive). For each location $\langle x, y \rangle$ and month m of each year (e.g., the
129 observed variance at coordinates $\langle -119.40, 49.94 \rangle$ in April 2005), we calculated the variance
130 in historical temperature data, for a total of $(2024 - 1998) \times 12 = 312$ observations per
131 location. We then modeled σ_T^2 a Generalized Additive Model (GAM) for Location and Scale
132 (GAMLS, Rigby & Stasinopoulos, 2005; Stasinopoulos & Rigby, 2007; section 7.9 in Wood,
133 2017) fitted with the `mgcv` package for `R` (v. 1.9-1, Wood, 2017). The linear predictor
134 for the location (i.e., the mean) included smooth terms of: each year's estimated within-
135 pixel monthly mean temperature ($\hat{\mu}_T$), month (m), a two-dimensional smooth of spatial
136 coordinates $\langle x, y \rangle$, and a tensor product interaction term of month and space to allow for
137 seasonal terms to vary smoothly over space. The linear predictor for the scale term, which
138 governs the mean-variance relationship (table 3.1 on p. 104 of Wood, 2017), included smooth
139 terms of the monthly mean temperature, month, and space. We did not include smooth terms
140 of year to avoid unrealistic projections when extrapolating beyond past 2023. The complete
141 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 and variance as specified by the gamma GMLS. For each month within each year from 2025 to 2100, we simulated hourly weather by including temperatures from the 0.1 to the 0.9 quantiles by increments of 0.1, and we weighted each quantile proportionally to the normalized Gaussian probability density for each quantile.

157 **2.1.3 Habitat rasters**

158 We estimated percent forest cover and distance from water using the temporally static
159 rasters created by Tuanmu & Jetz (2014). We calculated total forest cover by summing
160 the four rasters of evergreen/deciduous needle-leaf trees, evergreen broadleaf trees, decidu-
161 ous broadleaf trees, and mixed/other trees (raster classes 1-4, respectively). We converted
162 the raster of percent cover of open water (class 12) to a binary raster of pixels with water
163 ($\text{cover} \geq 1\% \approx 40,000\text{m}^2$ for a $\approx 4\text{km}^2$ pixel) or without water ($\text{cover} \leq 1\%$) and then
164 calculated each pixel's distance from the nearest pixel with water using the `distance()`
165 function from the `terra` package. We recognize that although this approach may fail to
166 account for small or ephemeral bodies of water, it should still capture large-scale prefer-
167 ences for proximity to water. Finally, we obtained two digital elevation models using the
168 `get_elev_raster()` function from the `elevatr` package (v. 0.99.0, Hollister *et al.*, 2023).
169 We used a raster with a zoom of 6 (a resolution of 0.009°) for model fitting and one with a
170 zoom of 3 (a resolution of 0.08°) for downloading climate change projections via `climatenar`.
171 All final rasters and code are available on GitHub (see the Data Availability Statement). For
172 ease of interpretability and comparison with current conditions, we assumed resources would
173 remain constant through to 2100, although we recognize that the spatial distribution of forest
174 cover and open water will change throughout the 21st century.

175 **2.2 Estimating mammals' instantaneous speeds**

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

183 The models were for one mountain goat, 15 boreal caribou, and two southern mountain
184 caribou (Table 1).

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

194 2.3 Estimating the effects of temperature on mammals' movement behaviour

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

206 To assess the importance of including temperature as an explicit covariate (as opposed
207 to including its effects with time of day and day of year), we fit models with and without
208 smooth effects of temperature and compared the fits of the two sets of models via analyses

209 of deviance (a form of generalized likelihood ratio tests) following the methods of Section
210 3.3 in Wood (2017). See Appendix B for additional information.

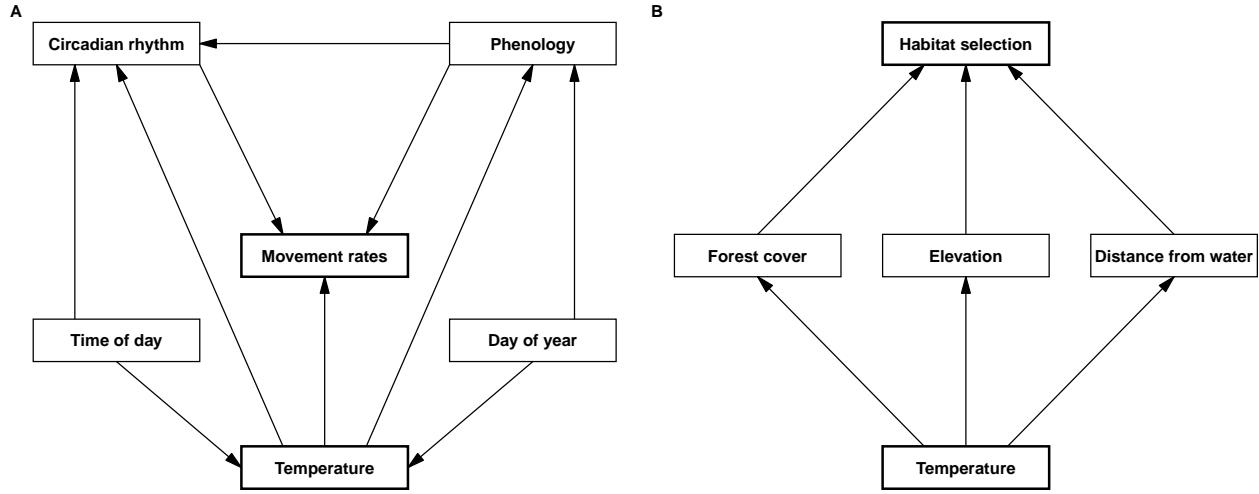


Figure 2: Directed Acyclical Graphs (DAGs) assumed for inferring the causal effects of temperature (red) on each species' movement behaviour. (A) Ambient temperature affects mammals' movement rates (i.e. probability of moving, speed when moving, and their product: hourly distance traveled). The effects 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.

211 2.3.1 Effects of temperature on movement rates

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

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

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

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

²⁴² while the model for movement speed when moving (i.e., $M = 1$, indicated with S) was

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

²⁴³ In both models, β_s indicates a fixed intercept for species s , Z_a indicates a Gaussian random
²⁴⁴ effect for animal a (of species s), $f_{j,s}$ indicates the j^{th} smooth function for species s , and
²⁴⁵ functions with two variables indicate tensor product interaction terms. The model code used
²⁴⁶ to fit the models is available in Appendix B.

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

²⁴⁸ We estimated the effects of temperature on each species' selection for percent forest
²⁴⁹ cover (`forest_perc`), elevation (`elevation_m`, in meters), and distance from water

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

263 Each species' model had the same structure:

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

264 where O indicates whether an animal was observed ($O = 1$) or not ($O = 0$), and the
 265 species-level indices are omitted for readability, but each term in the model can be as-
 266 sumed to be species-specific. Smooth effects of percent forest cover (`forest_perc`), eleva-
 267 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). 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			

293 Across all species, Relative Selection Strength (RSS) was weakest for forest cover and
 294 strongest for elevation. At temperatures near 0°C , boreal caribou selected for forest cover
 295 between 50% and 75%, elevations near 500 m above sea level, and distances from water <
 296 10 km, while southern mountain caribou selected for dense forest cover, elevations near 2
 297 km, and distances from water $\lesssim 5$ km. Cougars selected for dense forest cover ($> 75\%$),
 298 an elevation of ~ 1 km, and distances from water < 7.5 km. Elk selected for intermediate
 299 forest cover ($\approx 50\%$), elevations between 1 and 2 km, and distances from water of 10-15 km.
 300 Grizzly bears selected for relatively sparse forest cover (25-50%), elevation between 1 and 2
 301 km, and distances from water < 3 km. Mountain goats selected for sparse forest cover ($<$
 302 25%), elevations near 1.8 km, and distances from water < 5 km. Finally, wolves selected
 303 for forest cover ($\gtrapprox 50\%$), elevations near 1 km, and distances from water < 5 km. There was
 304 relatively strong agreement between models with and without temperature (Figs. B3, and
 305 B14), but including temperature always resulted in better fits (all p-values $< 2.2 \times 10^{-16}$; all
 306 $\Delta\text{AIC} \geq 342$; Appendix B). Accounting for temperature even resulted in a simpler HRSF

307 for mountain goats (lower model degrees of freedom due to simpler random smooth terms)
308 that fit the data better (lower deviance), and hence no test was necessary to show that the
309 inclusion of temperature produced a better fit.

310 **3.1 Effects of temperature on movement rates**

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

325 **3.2 Effects of temperature on habitat selection**

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

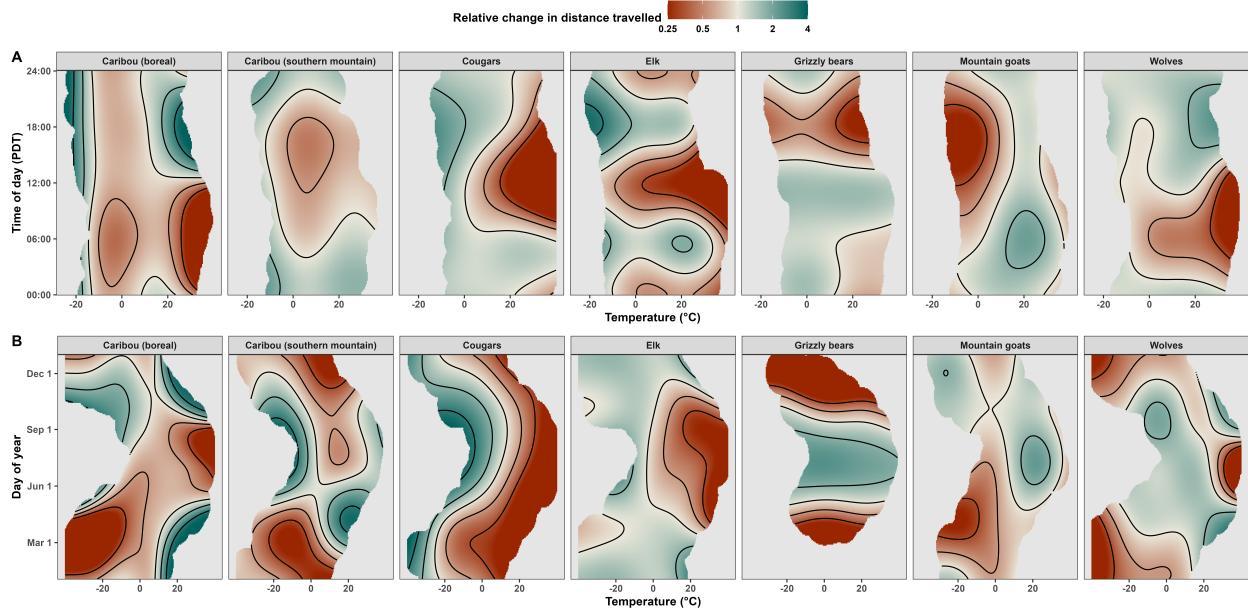


Figure 3: Temperature is a strong driver of how far and when mammals travel. The fill indicates the effects of temperature on the relative change in hourly distance travelled (probability of moving times mean speed when moving) over time of day on June 1st (**A**) and day of year at 12:00 PDT (**B**).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

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).

Fig. 5 presents the predicted habitat selection for boreal caribou and wolves. Overall,

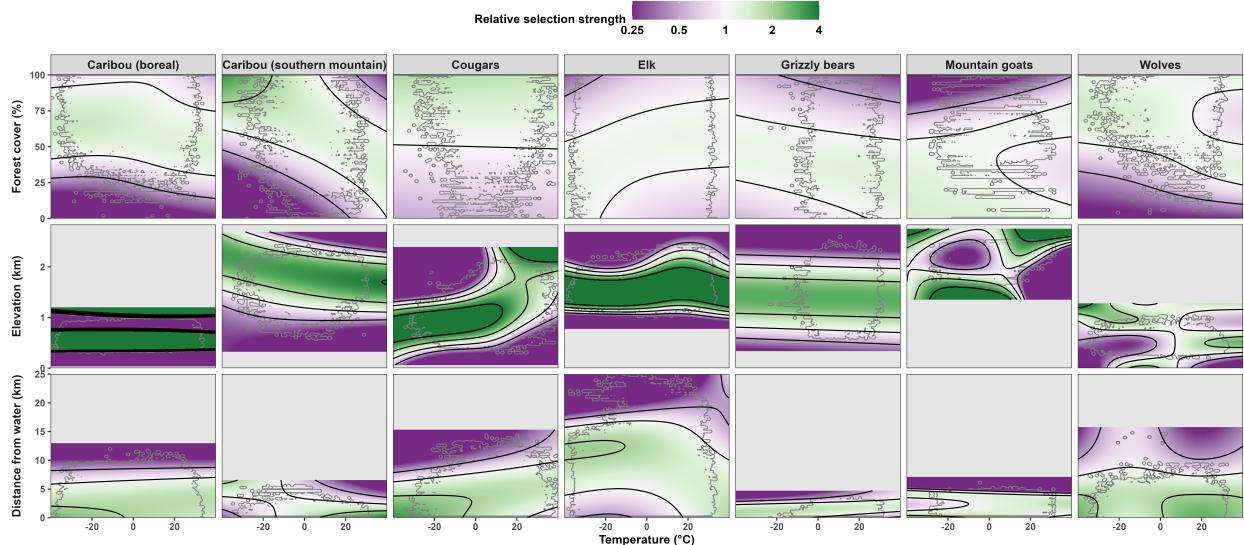


Figure 4: Mammals’ habitat selection depends on ambient temperature. Estimated relative selection strength (RSS) for forest cover (%), elevation (km), and distance from water (km) as a function of temperature. The grey contours indicate the extent of each species’ observed data. RSS values were re-centered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

346 both species selected for the same low-elevation area (< 500 m; Fig. 5A-B), but caribou
 347 generally avoided the river system that wolves were often found at, and their selection
 348 strength varied with temperature. As wolves’ habitat selection strengthened at warmer
 349 temperatures, co-occupancy at 20°C was approximately four times more higher than at -
 350 20°C, independent of changes in the species’ movement rates (Fig. 5C).

351 3.3 Predicted changes in movement behaviour during the 21st century

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

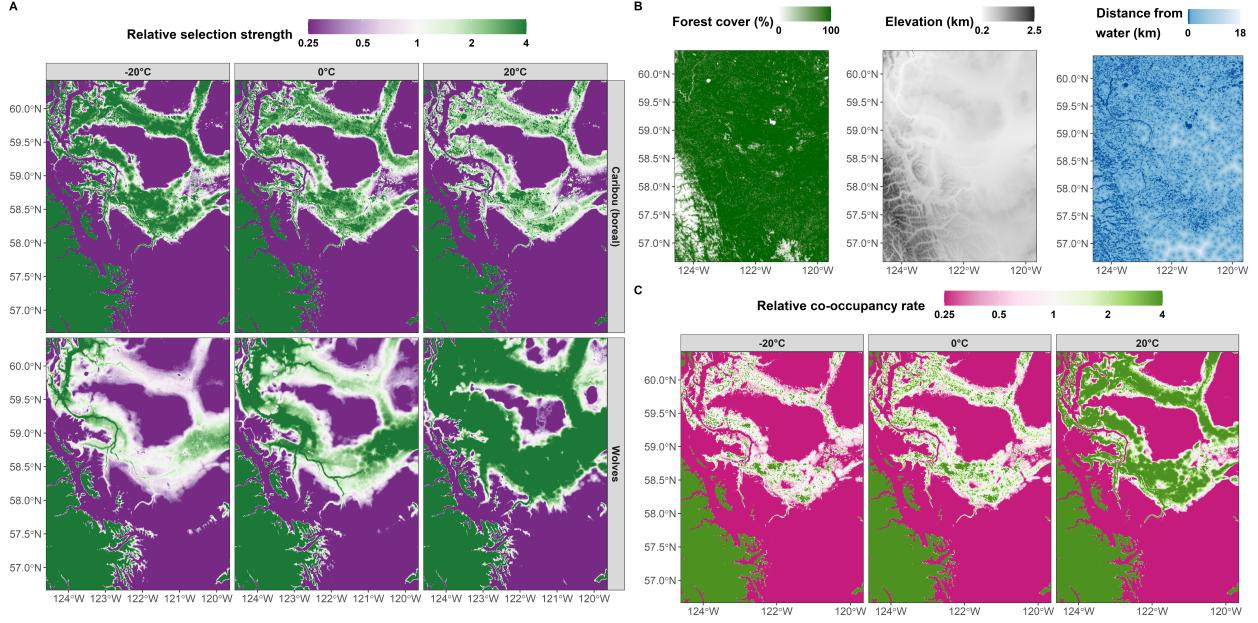


Figure 5: Temperature affects boreal caribou's and wolves' habitat selection and, consequently, their encounter rates. Panel (A) shows the rasters of the three habitat variables used in the hierarchical resource selection functions, while panel (B) shows the relative selection strength (RSS) for boreal 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.

361 early fall. Southern mountain caribou and mountain goats are projected to travel further by
 362 2100, although the estimates for southern mountain caribou varied greatly over space (Fig.
 363 7). Cougars, elk, and wolves were projected to move less by 2100, with cougars showing as
 364 much as a 24% decrease in mean yearly distance travelled.

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

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

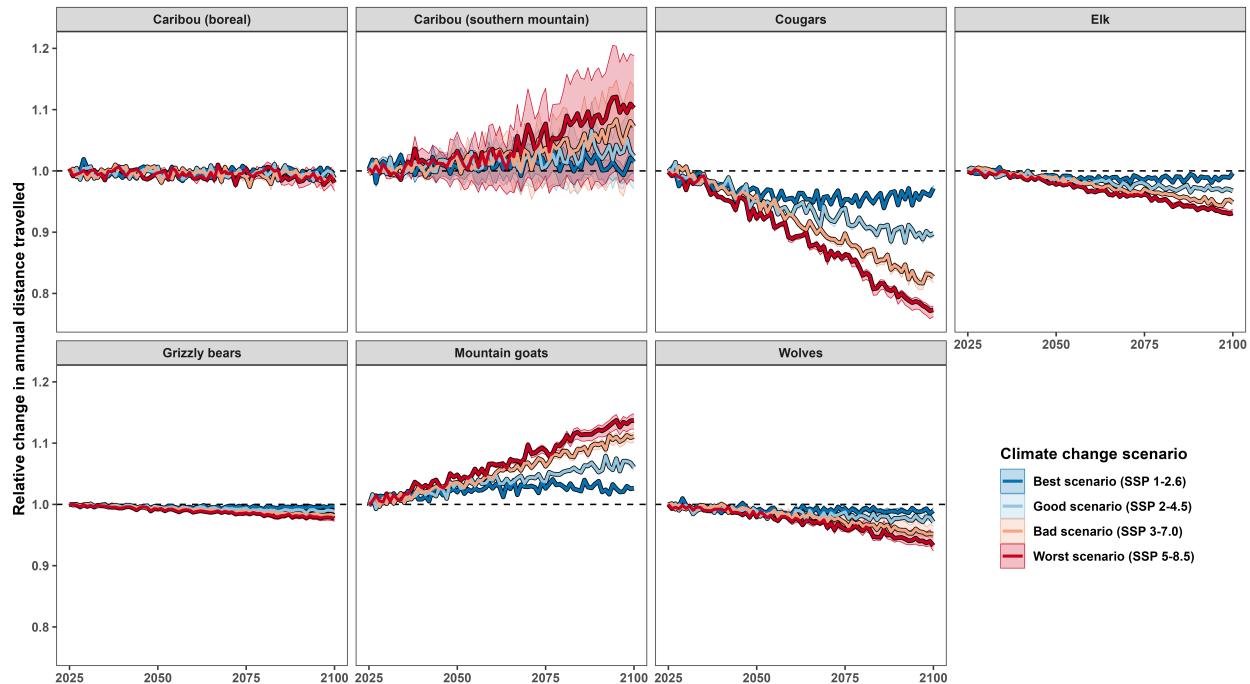


Figure 6: Species are predicted to alter their movement rates differently in response to climate change, and worse climate-change scenarios will result in the greatest change. Bold lines indicate the median change in yearly distance travelled (probability of moving times speed when moving) due to predicted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

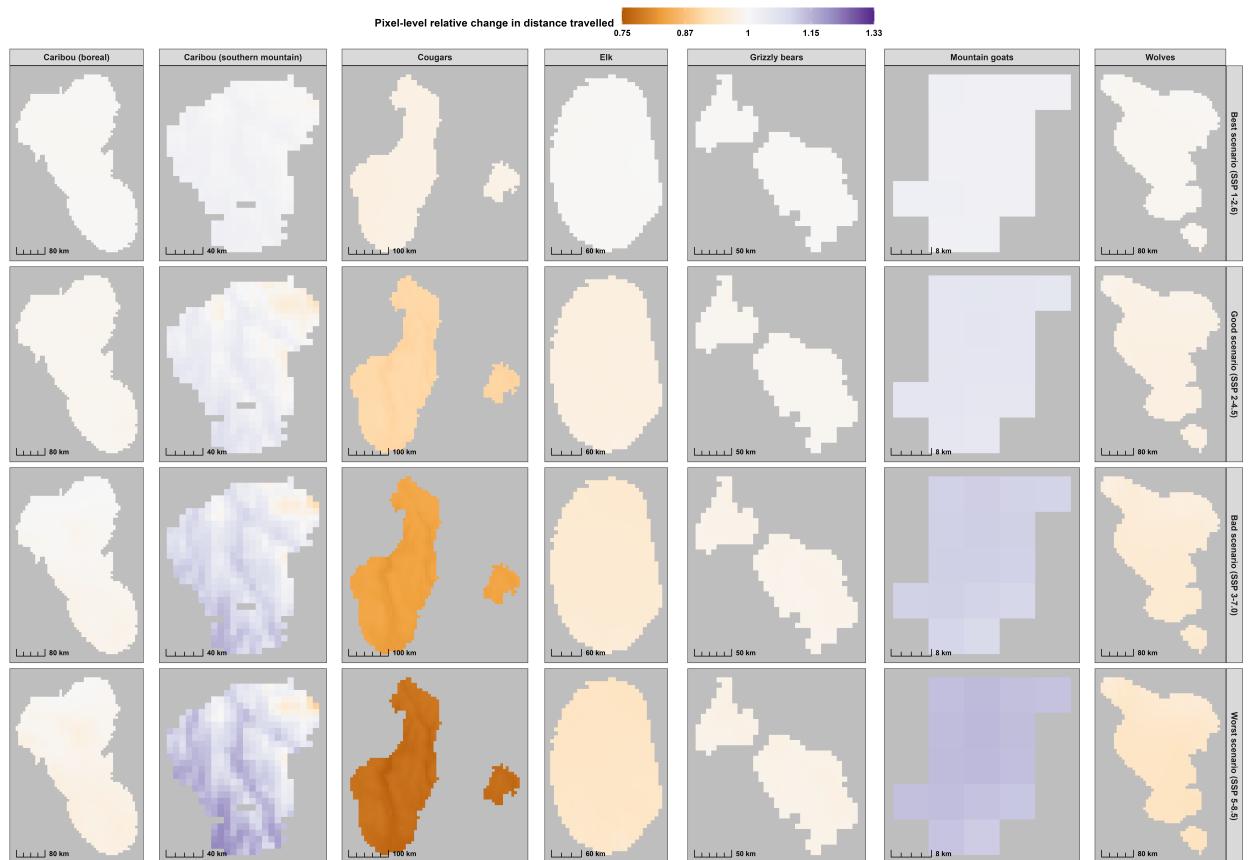


Figure 7: Climate change is predicted to impact each species' movement rates differently, but changes will also vary spatially. The color of each pixel indicates the predicted changes in distance traveled in 2100 at that pixel, relative to the value in 2025, averaged across all four scenarios. Values < 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).

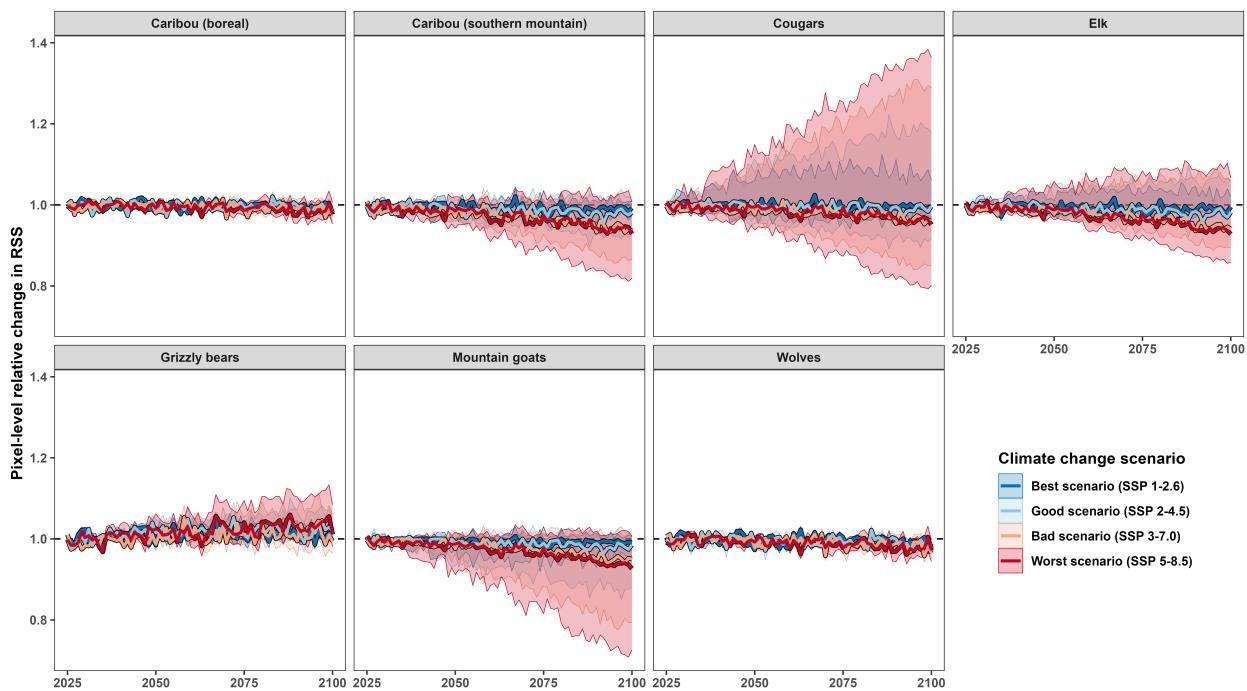


Figure 8: Species are predicted to alter their habitat selection differently in response to climate change, and worse climate-change scenarios will result in the greatest change. Bold lines indicate the change in median RSS due to predicted changes in temperature within each species' study area. Shaded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

382 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).

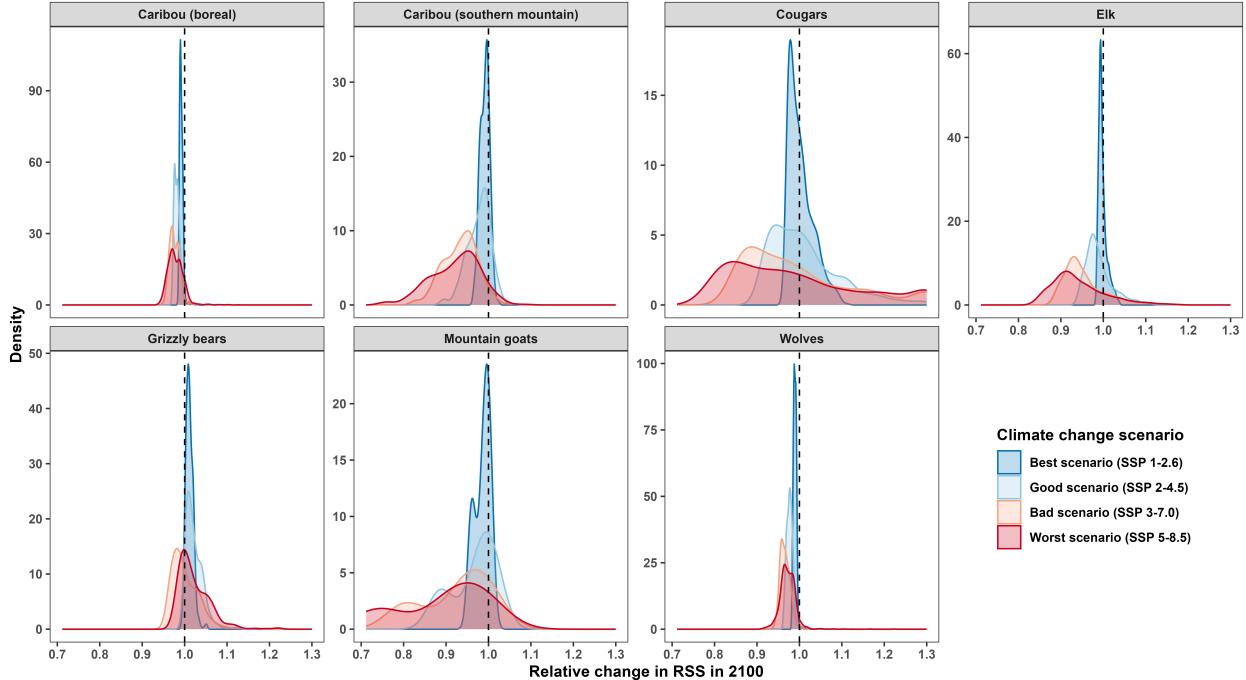


Figure 10: Climate change is predicted to cause species to decrease their selection strength for their current habitats, and worse climate change scenarios will have the greatest impact. The density plots indicate each species’ change in RSS in 2100 for their current habitat (Fig. 8), relative to each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

386 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

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

411 The effects of warming temperatures on movement rates varied across species, seasons,
412 and space due to differences in species' behavior and physiology as well as their habitats'
413 phenology (e.g., the timing of green-up). For boreal caribou, hotter temperatures decreased
414 movement rates summer but increased them otherwise, mirroring previous studies (Stien
415 *et al.*, 2012; Leclerc *et al.*, 2021; Lessard *et al.*, 2025). The increase in movement rates
416 with temperature during the cold months is likely partly due to shallower snow depth,
417 which results in greater mobility (Pedersen *et al.*, 2021), but warmer temperatures during
418 snowy seasons also increase the risk of temperature fluctuations near 0°C and the risk of
419 rain-on-snow events (Musselman *et al.*, 2018), which limit forage availability and increase
420 time spent foraging (Stien *et al.*, 2012; Berger *et al.*, 2018; Mezzini *et al.*, 2025). The
421 reduced movement rates during warmer summers are likely mainly due to more frequent
422 resting and use of thermal refugia, given ungulates' documented risk of hyperthermia (Alston
423 *et al.*, 2020; Verzuh *et al.*, 2023). Therefore, although we predict that boreal caribou's
424 yearly average movement rates will remain approximately unchanged throughout the 21st
425 century, the projections do not show the changes in seasonal movement phenology. This is an

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

433 Boreal wolves responded to temperature similarly to boreal caribou, and habitat selection
434 strength was not projected to change noticeably by 2100, but wolves were predicted to move
435 less in future decades. In contrast, cougars showed markedly different seasonal responses
436 to temperature, with warmer temperatures always resulting in less travel, which resulted
437 in strong predicted decreases in movement rates over the 21st century. However, spatial
438 heterogeneity in habitat, climate, and cougar behaviour may cause boreal individuals to
439 respond to temperature differently from those in our study. Still, rising temperatures clearly
440 affect more than each individual species' movement behaviour; they have complex effects
441 on entire communities and their trophic structures. Cunningham *et al.* (2021) discuss the
442 importance of adopting a community-level perspective when assessing the effects of climate
443 change on animals' movement behaviour and phenology. For example, as temperatures
444 warm and both boreal caribou and wolves increase their movement rates in fall, winter, and
445 spring, they also increase their encounter rates (Martinez-Garcia *et al.*, 2020), which will
446 likely increase predation risk when caribou are pregnant or with young calves. Additionally,
447 while both species saw reduced movement rates during hot summer days, boreal wolves' use
448 of anthropogenic linear features (e.g., roads, seismic lines) may allow them to reduce the
449 total thermal costs of movement by moving for shorter periods while increasing the chances
450 of encountering heat-stressed prey (Whittington *et al.*, 2011; Dickie *et al.*, 2017; Dickie *et al.*,
451 2022). Furthermore, caribou that attempt to reduce predation risk from wolves by avoiding
452 wolf habitat may still risk increasing predation pressure from bears, cougars, and coyote

453 (Leblond *et al.*, 2016; DeMars *et al.*, 2023; Labadie *et al.*, 2023).

454 Considerations about changes in trophic interactions leads to another important caveat
455 about the results we present. The estimated changes in movement behaviour cannot be fully
456 attributed to physiological responses to temperature alone, since other aspects of habitats'
457 seasonal phenology are (nonlinearly) correlated with temperature. For example, mountain
458 goats' lower movement rates at temperatures near 0°C in winter may be due to a multitude
459 of factors, including: increased movement difficulty, since melting snow and rain-on-snow
460 events increase the energetic costs of movement (White, 2025); reduced movement during
461 storms (Musselman *et al.*, 2018); and increased encounter risk with predators (Sullender
462 *et al.*, 2023). However, milder temperatures can also increase plant growth, which allows
463 goats to spend more time foraging within and less time travelling across patches (Charnov,
464 1976; White *et al.*, 2025). Therefore, Fig. 3 illustrates an estimate of the total effects of
465 temperature on each species' movement rates, but it does not explicitly account for energetic
466 costs. Similarly, species' changes in habitat selection do not explicitly account for any changes
467 in physiological or energetic costs. Additionally, forest cover, elevation, and distance from
468 water are often correlated, so the estimated effects should be interpreted carefully, and they
469 may not be applicable outside the study areas used here. For example, both mountain goats
470 and elk selected for higher elevation as temperatures warmed, but our models did not account
471 for differences in forage availability at different elevations.

472 Climate change has also had extensive impacts on plant growth and phenology (Cleland
473 *et al.*, 2007; Denny, 2019; Tysor, 2025) with consequences on herbivores' behaviour and
474 fitness (Post & Forchhammer, 2008; Aikens *et al.*, 2017). Plants' limited ability to disperse
475 to and establish in new habitats is often a limiting factor for herbivores' ability to escape
476 hotter temperatures by moving to higher altitudes or latitudes, and the advance of herbivores
477 can further limit plants' ability to establish (Speed *et al.*, 2012; Diffenbaugh & Field, 2013).
478 Consequently, mammals that move to higher elevations may be forced to spend more time
479 foraging if forage is scarce or unpredictable (Mezzini *et al.*, 2025), which will increase both

their energetic expenditure and encounter rates with predators and competitors (Kohl *et al.*, 2019; Martinez-Garcia *et al.*, 2020; Tórrez-Herrera *et al.*, 2020; Smith *et al.*, 2023). If local peaks become unsuitable habitat, and moving to nearby higher peaks requires traveling across low-quality and high-risk habitat (Fig. 9), habitat fragmentation may prevent movement across ranges (White *et al.*, 2025).

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

Accelerating multifarious change in species' movement behaviour and energetic costs require conservation measures that are proactive and anticipate future changes. Polazzo *et al.* (2024) present a framework for estimating species' responses to multifarious change using GAMs that is particularly useful when estimating species' (nonlinear) responses to interactions between environmental variables (e.g., changes in both temperature and limiting nutrients). By accounting for the effects of multiple variables at once, they demonstrate how a species' response to one variable can depend on other concurrent changes. Estimating responses to multifarious change is crucial in assessing mammals' responses to hotter temperatures, altered phenology, and novel community dynamics. For instance, warming temperatures have increased exposure to disease and parasites, with impacts on mammalian

507 physiology and energetic needs (Pickles *et al.*, 2013; Barber *et al.*, 2018; Blanchong *et al.*,
508 2018; Gray & Ogden, 2021; Gude *et al.*, 2022). In particular, severe tick loads can reduce
509 mammals' ability to thermoregulate in the cold due to reduced body fat and fur (Pekins,
510 2020) and can even reduce movement rates by increasing time spent recumbent (Addison *et*
511 *al.*, 2023).

512 Protected areas must support populations not only in present conditions but also as
513 species' needs and behaviour change over the decades (Simmons *et al.*, 2021; Livingstone *et*
514 *al.*, 2023). Recent evidence has questioned whether current protected areas will be effective
515 in the long term (Loarie *et al.*, 2009; Diffenbaugh & Field, 2013; Williams & Blois, 2018),
516 and increasingly more experts have been calling for proactive and long-term conservation.
517 By identifying and actively protecting climate change refugia and corridors, we may be able
518 to reduce the effects of climate change on mammalian movement behaviour and community-
519 level responses and ensure that protected areas may be viable for decades to come (Michalak
520 *et al.*, 2018; Graham *et al.*, 2019; Stralberg *et al.*, 2020; Hua *et al.*, 2022).

521 Future work should develop models that account for covariates that are specific to the
522 study species and area, such as forest age and disturbance (DeMars *et al.*, 2023), terrain
523 ruggedness (White & Gregovich, 2017), anthropogenic linear features (Dickie *et al.*, 2017),
524 greater physiological stress from infection and parasitism (Pickles *et al.*, 2013; Gude *et al.*,
525 2022), and growing human presence in wild spaces (Sih *et al.*, 2011; Rice, 2022), including
526 the growing risk of human-wildlife conflict (Abrahms *et al.*, 2023; Weststrate *et al.*, 2024). In
527 particular, forests in western Canada are highly dynamic over time (Zhang *et al.*, 2015), and
528 fires size and burn severity have increased in western Canada in recent decades (Whitman *et*
529 *al.*, 2022; Parisien *et al.*, 2023; Wang *et al.*, 2025). Thus, while our use of a static raster of
530 forest cover allowed for simpler models and climate change projections, future studies should
531 account for mammals' responses to temporal forest dynamics, including the impacts of fire
532 (Whitman *et al.*, 2022; Parisien *et al.*, 2023; Wang *et al.*, 2025), logging (Lochhead *et al.*,
533 2022) and other extractive industries (Dickie *et al.*, 2017, 2024). Additionally, rising inci-

534 dence of disease and parasite load over the coming decades may also alter increase mammals'
535 energetic needs (Gude *et al.*, 2022) and time spent foraging or hunting (Mezzini *et al.*, 2025).
536 However, the inclusion of temporally dynamic variables will require that any future projec-
537 tions of species' behaviour depend on temporally dynamic estimates of how such variables
538 will change over the years.

539 We have demonstrated that temperature has complex and nonlinear effects on how and
540 where boreal mammals move. Rising temperatures have impacted mammals' daily and sea-
541 sonal movement cycles, and changes are expected to intensify throughout the 21st century.
542 Quantifying how temperature affects mammalian behavior and fitness is a first step towards
543 developing an understanding of the effects of climate change on landscape dynamics and the
544 effectiveness of protected areas in the future. By leveraging the flexibility and statistical
545 power of Hierarchical Generalized Additive Models, we have provided researchers with mal-
546 leable and data-driven methods for assessing species' responses to climate change. We hope
547 that future work will develop more species-specific models with the intent of developing a
548 community-level framework for quantifying and predicting how communities will respond to
549 climate change.

550

551 **Author contributions**

552 SM performed the data cleaning, ran the analyses, and wrote the manuscript. CHF wrote
553 code for estimating instantaneous movement speeds. MJN conceived of the project idea and
554 supervised SM throughout the project. All other authors contributed telemetry data and/or
555 reviewed the interpretation of the results for their species of interest. KH and SD contributed
556 substantially to manuscript review. All authors contributed to reviewing the manuscript.

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