

Rising temperatures alter how and where mammals move

Stefano Mezzini^{1,2} Christen H. Fleming^{3,4} Karen E. Hodges^{1,2}

Siobhan Darlington^{1,2} Adam T. Ford^{1,2} TJ Gooliaff⁵

Robert Serrouya^{1,2,6} Michael J. Noonan^{1,2,7}

¹ Okanagan Institute for Biodiversity, Resilience, and Ecosystem Services, The University of British Columbia Okanagan, Kelowna, British Columbia, Canada.

² Department of Biology, The University of British Columbia Okanagan, Kelowna, British Columbia, Canada.

³ Department of Biology, University of Central Florida, Orlando, Florida 32816, United States.

⁴ Smithsonian Conservation Biology Institute, National Zoological Park, 1500 Remount Rd., Front Royal, VA 22630, United States.

⁵ British Columbia Ministry of Forests, Lands, Natural Resource Operations and Rural Development, Penticton, BC, Canada.

⁶ Wildlife Science Centre, Biodiversity Pathways, University of British Columbia Okanagan, Revelstoke, British Columbia, Canada.

⁷ Department of Computer Science, Math, Physics, and Statistics, The University of British Columbia Okanagan, Kelowna, British Columbia, Canada.

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Contact Information: *Corresponding author's telephone, and email details*

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 unclear how temperature will impact mammals' movement behaviour throughout the 21st century and important seasonal cycles such as migration. 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 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 elevation. 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 allows for a rapid response to a variety of stimuli (Nathan *et*
³ *al.*, 2008). Animals move to optimize resource use (e.g., food, water, shelter; Charnov, 1976;
⁴ Kacelnik *et al.*, 1992; Merkle *et al.*, 2016; Mezzini *et al.*, 2025), optimize habitat use (Winter
⁵ *et al.*, 2024), and avoid predators and competitors (Tórrez-Herrera *et al.*, 2020; Peterson *et*
⁶ *al.*, 2021; Bartashevich *et al.*, 2024; Tan *et al.*, 2024). How and where animals move thus also
⁷ determines encounter rates with resources (Mezzini *et al.*, 2025), humans (Johnson *et al.*,
⁸ 2018; Weststrate *et al.*, 2024), and predators, prey, and competitors (Martinez-Garcia *et al.*,
⁹ 2020; Glass *et al.*, 2021; Brivio *et al.*, 2024), including infected and parasitized individuals
¹⁰ (Blanchong *et al.*, 2018). However, ambient temperature affects animals' movement rates
¹¹ by altering the energetic cost of movement and thermoregulation (McNab, 1970; Taylor *et*
¹² *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 (Pigeon *et*
¹⁴ *al.*, 2016; Johnson *et al.*, 2018; Carbeck *et al.*, 2022; but see McLellan & McLellan, 2015),
¹⁵ and life history (Woodroffe *et al.*, 2017; Newediuk *et al.*, 2024), and even cause physiological
¹⁶ damage and death (Heten *et al.*, 2014; Powers *et al.*, 2017; Ratnayake *et al.*, 2019; Schmidt
¹⁷ *et al.*, 2020; Rabaiotti *et al.*, 2021; Schwerdt *et al.*, 2024). Animals may search for a short-
¹⁸ term buffer from extreme temperatures by moving to thermal refugia (Hannah *et al.*, 2014;
¹⁹ Elmore *et al.*, 2017; Attias *et al.*, 2018; Arechavala-Lopez *et al.*, 2019; Gulland *et al.*, 2022),
²⁰ and shelter may even be preferred over forage abundance (Hall *et al.*, 2016). However,
²¹ climate change during the last century (IPCC, 2023) has caused animals to alter how and
²² where they move as they respond to hotter temperatures and increasingly severe and frequent
²³ extreme-heat events (Bunnell *et 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). Mammals can mitigate the effects of temperature by altering their movement behavior, including the timing of migration (Leclerc *et al.*, 2021; Xu *et al.*, 2021) and their hunting strategies (Creel *et al.*, 2016; Rabaiotti & Woodroffe, 2019), but a species' movement behavior is often constrained by its body size and vagility, including its main method of locomotion (Webber & McGuire, 2022).

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; Woodroffe *et al.*, 2017; Guiden & Orrock, 2020; 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).

54 As heat stress intensifies throughout the 21st century, mammals will continue to suffer
55 impacts on their fitness, movement rates, and habitat selection (Deb *et al.*, 2020; Woo-
56 Durand *et al.*, 2020). It remains unclear how or whether species will be able to respond to
57 climate change in the current century (Deb *et al.*, 2020; Woo-Durand *et al.*, 2020; Verzuh
58 *et al.*, 2023), especially if populations fail to adapt (Botero *et al.*, 2015; Sawyer *et al.*, 2019)
59 or are physiologically incapable to do so (Sherwood & Huber, 2010; Botero *et al.*, 2015;
60 Williams & Blois, 2018). Recent work has documented the effects of climate change on
61 mammals' ranges (Leclerc *et al.*, 2021), thermoregulation (Mota-Rojas *et al.*, 2021), and
62 movement behaviour (McCain, 2019; Cunningham *et al.*, 2021; Melin *et al.*, 2023), but there
63 remains a need for fine-scale estimates of the effects of temperature on mammals' movement
64 behaviour and quantitative predictions of future changes in movement behaviour.

65 In this paper, we quantify the effects of proximal air temperature on mammalian move-
66 ment behaviour, namely movement rates and habitat selection of six large-bodied terrestrial
67 mammal species in western Canada (boreal and southern mountain caribou, cougars: *Puma*
68 *concolor*, elk: *Cervus canadensis*, grizzly bears: *Ursus arctos horribilis*, mountain goats, and
69 wolves; Table 1). Western Canada is currently experiencing accelerating and widespread
70 but spatially heterogeneous warming (Turner & Clifton, 2009; Kienzle, 2018; Dierauer *et*
71 *al.*, 2021), phenological shifts (plants: Post & Forchhammer, 2008; Tysor, 2025; ice: Basu
72 *et al.*, 2024; caribou: Le Corre *et al.*, 2016), and more frequent and intense extreme heat
73 events (Zhang *et al.*, 2023). Decision makers must understand which areas will best sustain
74 and protect biodiversity not only for current conditions but future decades, too. Failing to
75 understand how climate change will affect mammalian movement behaviour will hinder our
76 ability to respond to the current climate crisis and make decisions that are viable in the
77 long term. Furthermore, understanding how temperature affects individual species is the
78 first step towards understanding how temperature impacts the community dynamics (Hegel
79 *et al.*, 2010; Stien *et al.*, 2012; Pokallus & Pauli, 2015; Cunningham *et al.*, 2021; Carbeck *et*
80 *al.*, 2022) and phenology (Bunnell *et al.*, 2011; Duncan *et al.*, 2012; Le Corre *et al.*, 2016;

81 Merkle *et al.*, 2016; Slatyer *et al.*, 2022; Gerlich *et al.*, 2025), and how these changes will
 82 impact mammals in the coming decades (Sobie *et al.*, 2021; Eum *et al.*, 2023; Weststrate *et*
 83 *al.*, 2024).

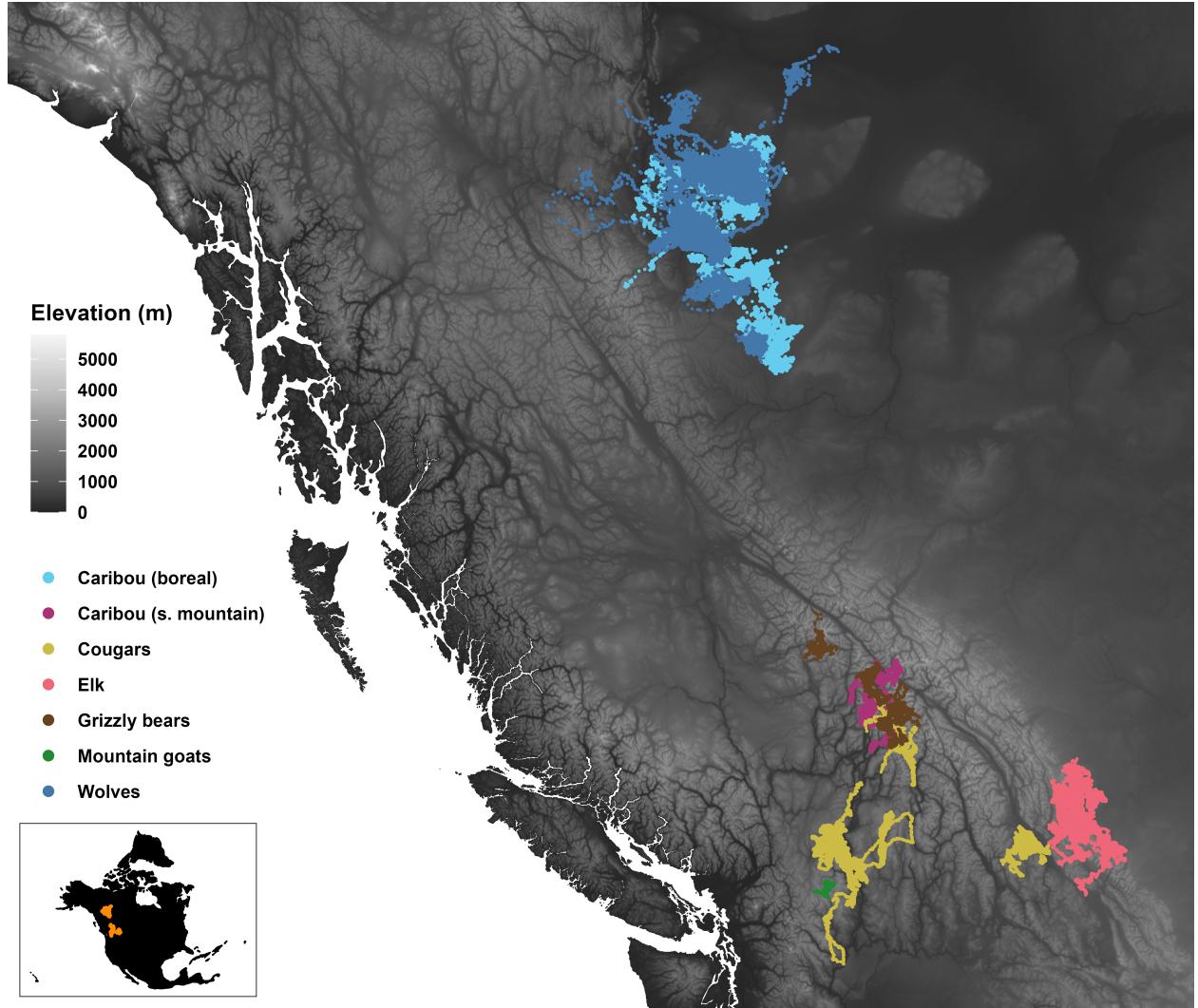


Figure 1: GPS telemetry data for the six species in this study (dots) over a digital elevation model for the study area. The inset in the bottom left shows the telemetry data within the north american continent. Both maps use the BC Albers Equal Area Conic projection (EPSG:3005).

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

Species	Start	End	Fixes	Δt (hours)	Animals	Has speed
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

84 2 Methods

85 2.1 Datasets used

86 In this study, we estimate how temperature affected mammals' probability of moving,
 87 speed when moving, and habitat selection by leveraging three datasets: (1) a multi-species
 88 collection of 25 years of GPS telemetry data throughout a large spatial range of western
 89 Canada (Fig. 1), (2) historical, hourly air temperature data from the ERA5 reanalyzed
 90 dataset (Hersbach *et al.*, 2023), and (3) temporally static rasters of percent forest cover,
 91 elevation, and distance from water. We then forecast each species' movement behaviour
 92 throughout the 21st century using monthly climate change projections under four Shared
 93 Socioeconomic Pathways (SSPs; Riahi *et al.*, 2017; Mahony *et al.*, 2022): SSP 1-2.6 ("Sus-
 94 tainability – Taking the Green Road"; low challenges to mitigation and adaptation), SSP
 95 2-4.5 ("Middle of the Road: medium challenges to mitigation and adaptation"), SSP 3-7.0
 96 ("Regional Rivalry – A Rocky Road"; high challenges to mitigation and adaptation), and
 97 SSP 5-8.5 ("Fossil-fueled Development – Taking the Highway"; high challenges to mitigation,
 98 low challenges to adaptation).

99 We acknowledge that our models of habitat selection ignore many important variables of
 100 habitat selection (e.g., forest type, structure, and age; terrain slope and aspect; prey avail-
 101 ability; population density). We limited our models to only use three simple and temporally
 102 static rasters to produce simple and easily interpretable estimates and forecasts under the
 103 assumption of temporally invariant landscapes.

¹⁰⁴ **2.1.1 GPS telemetry data**

¹⁰⁵ Boreal caribou and wolf telemetry data were acquired from a data repository of the British
¹⁰⁶ Columbia Oil and Gas Research and Innovation Society (BC ORGIS) that was collected as
¹⁰⁷ part of the boreal caribou radio-collaring program of the BC OGRIS Research and Effec-
¹⁰⁸ tiveness Monitoring Board (REMB; BC OGRIS, 2018). Southern mountain caribou data
¹⁰⁹ were obtained from Ford *et al.* (2023). Cougar data are from Darlington *et al.* (2025) and
¹¹⁰ (**serrouya_ref?**). Elk data from the work of Ciuti *et al.* (2012) were downloaded from
¹¹¹ Movebank (Kays *et al.*, 2022). Finally, grizzly bear telemetry data are from Serrouya *et al.*
¹¹² (2011), while mountain goat data are from the work of Balyx (2022) and were provided by
¹¹³ the British Columbia Ministry of Environment and Parks.

¹¹⁴ From the full set of telemetry data, we removed 2,396 problematic GPS locations (0.16%,
¹¹⁵ including collar calibration data) after inspecting diagnostic plots of (1) distance from the
¹¹⁶ median location, (2) straight-line displacement between locations, (3) turning angle, and
¹¹⁷ (4) time interval between consecutive points. Particular attention was paid to points with
¹¹⁸ large turning angles ($\gtrapprox 170^\circ$) and excessively high straight-line displacement, especially if
¹¹⁹ antecedent and subsequent points indicated relatively stationary behaviour (Appendix A).

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

¹²¹ Rasters of hourly air temperature data were downloaded from the ERA5 database (Hers-
¹²² bach *et al.*, 2023) from the European Center for Medium-range Weather Forecasting server
¹²³ (ECMWF; www.ecmwf.int; <https://cds.climate.copernicus.eu>). Proximal air temperature
¹²⁴ was estimated for each location by extracting the value from the corresponding raster cell
¹²⁵ from the temporally nearest raster using the `extract()` function from the `terra` package
¹²⁶ (v. 1.7-46, Hijmans, 2023) for `R` (R Core Team, 2024).

¹²⁷ To obtain projected average monthly temperatures from 2025 to 2100 at a 0.08° spatial
¹²⁸ resolution, we used the `climatenaR` package (v. 1.0, Burnett, 2023) for `R` and ClimateNA
¹²⁹ v. 7.4.2 (Wang *et al.*, 2016; Mahony *et al.*, 2022). However, the climate projections only

130 included estimates of future monthly averages, a scale substantially coarser than that of our
131 tracking data (Table 1). To estimate the distribution of temperatures at an hourly scale
132 within a month, we assumed values to be approximately normally distributed with mean μ_T
133 and variance σ_T^2 . We estimated μ_T using the ClimateNA projections, while we estimated
134 σ_T^2 by modeling the observed variance in historical weather data for western Canada from
135 1998 to 2023 (inclusive). For each location $\langle x, y \rangle$ and month m of each year (e.g., the
136 observed variance at coordinates $\langle -119.40, 49.94 \rangle$ in April 2005), we calculated the variance
137 in historical temperature data, for a total of $(2024 - 1998) \times 12 = 312$ observations per
138 location. We then modeled σ_T^2 a Generalized Additive Model (GAM) for Location and Scale
139 (GAMLS, Rigby & Stasinopoulos, 2005; Stasinopoulos & Rigby, 2007; section 7.9 in Wood,
140 2017) fitted with the `mgcv` package for R (v. 1.9-1, Wood, 2017). The linear predictor
141 for the location (i.e., the mean) included smooth terms of: each year's estimated within-
142 pixel monthly mean temperature ($\hat{\mu}_T$), month (m), a two-dimensional smooth of spatial
143 coordinates $\langle x, y \rangle$, and a tensor product interaction term of month and space to allow for
144 seasonal terms to vary smoothly over space. The linear predictor for the scale term, which
145 governs the mean-variance relationship (table 3.1 on p. 104 of Wood, 2017), included smooth
146 terms of the monthly mean temperature, month, and space. We did not include smooth terms
147 of year to avoid unrealistic projections when extrapolating beyond past 2023. The complete
148 model for the distribution of projected temperature was thus

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

149 where $\mu_{\sigma_T^2}$ and $\nu_{\sigma_T^2}$ indicate the location and scale parameters of the gamma distribution of
 150 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
 151 $f_{S,j}$ indicate the j^{th} smooth functions for the location and scale parameters, respectively.
 152 To ensure the smooth functions of month, $f_{L,2}(m)$ and $f_{S,2}(m)$, joined smoothly between
 153 December and January, the terms use cyclic cubic spline bases. The spatial terms used two-
 154 dimensional Duchon splines, a generalization of thin-plate regression splines (p. 221 of Wood
 155 (2017)). The smoothness parameters were estimated via REstricted Maximum Likelihood
 156 (REML; p. 83 of Wood, 2017). See the Data Availability Statement for additional information
 157 on the code used to fit the model.

158 We simulated hourly variation in future years by assuming hourly temperature followed
 159 a normal distribution with mean specified by the monthly **climatenaR** climate projections
 160 and variance as specified by the gamma GMLS. For each month within each year from
 161 2025 to 2100, we simulated hourly weather by including temperatures from the 0.1 to the
 162 0.9 quantiles by increments of 0.1, and we weighted each quantile proportionally to the
 163 normalized Gaussian probability density for each quantile.

164 **2.1.3 Habitat rasters**

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

182 **2.2 Estimating mammals' instantaneous speeds**

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

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

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

201 2.3 Estimating the effects of temperature on mammals' movement behaviour

202 Ambient temperature is only one of the many drivers of mammalian movement behaviour
203 (Fig. 2). Many species alter their movement rates (e.g., movement frequency and speed)
204 daily or seasonally in response in factors such as solar time, photoperiod, forage availability,
205 reproductive cycles, and predator avoidance. Similarly, ambient temperature also fluctuates
206 throughout the day and across seasons. Therefore, estimating the effects of temperature
207 on movement rates requires accounting for how mammals' response to temperature changes
208 with time of day and day of year (Webb *et al.*, 2010; Fig. 2A; Péron *et al.*, 2017; Buderman *et*
209 *al.*, 2018; Guiden & Orrock, 2020; Leclerc *et al.*, 2021; Xu *et al.*, 2021). Similarly, mammals'
210 selection strength for resources depends on ambient temperature, since higher temperatures
211 can promote a selection for refuge from heat (e.g., thicker forest cover, higher elevation,
212 proximity to water; Attias *et al.*, 2018; Giroux *et al.*, 2023).

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

216 of deviance (a form of generalized likelihood ratio tests) following the methods of Section
217 3.3 in Wood (2017). See Appendix B for additional information.

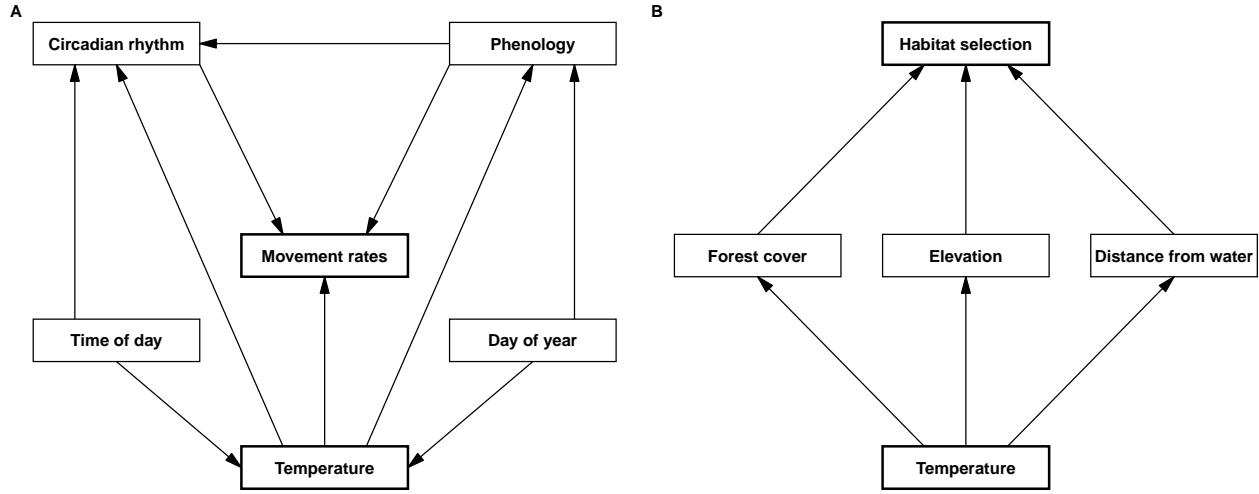


Figure 2: Directed Acyclical Graphs (DAGs) assumed for inferring the causal effects of temperature (red) on each species' movement behaviour. (A) Ambient temperature affects mammals' movement rates (i.e. probability of moving, speed when moving, and their product: hourly distance traveled). The effects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

218 2.3.1 Effects of temperature on movement rates

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

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

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

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

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

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

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

254 **2.3.2 Effects of temperature on habitat selection**

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

257 (`dist_water_m`, in meters) by fitting a Hierarchical Resource Selection Function (HRSF) for
 258 each species (McCabe *et al.*, 2021). We fit each HRSF using an HGAM with a Poisson family
 259 of distributions and log link function (Appendix B; Aarts *et al.*, 2008). After removing
 260 non-resident individuals (Table B1), we accounted for the spatiotemporal autocorrelation
 261 in the telemetry locations by weighting each point based on the telemetry's Autocorrelated
 262 Kernel Density Estimate (Fleming & Calabrese, 2017; Noonan *et al.*, 2019b; Alston *et al.*,
 263 2022) to produce estimates of second-order habitat selection (Johnson, 1980). Quadrature
 264 points were used to approximate the likelihood function of a Poisson point process through
 265 Monte-Carlo Markov chain-based integration (Aarts *et al.*, 2008; Fithian & Hastie, 2013;
 266 Baddeley *et al.*, 2015) and were determined using the raster cells in each animal's 99.9%
 267 AKDE percentile, with each raster cell having a weight of 1. The number of quadrature
 268 locations greatly outnumbered the number of observed locations (Fig. B12), especially after
 269 accounting for the AKDE weights (Fig. B13).

270 Each species' model had the same structure:

$$\left\{ \begin{array}{l} O \sim \text{Pois}(\lambda) \\ \mathbb{E}(O) = \mathbb{V}(O) = \lambda \\ \log(\lambda) = \beta_0 + f_1(\text{forest_perc}) + f_2(\text{elevation_m}) + f_3(\text{dist_water_m}) + \\ Z_a + f_{4,a}(\text{forest_perc}) + f_{5,a}(\text{elevation_m}) + f_{6,a}(\text{dist_water_m}) + \\ f_7(\text{forest_perc}, \text{temp_c}) + f_8(\text{elevation_m}, \text{temp_c}) + \\ f_9(\text{dist_water_m}, \text{temp_c}) + f_{10}(\text{temp_c}) + f_{11,a}(\text{temp_c}) \end{array} \right. , \quad (4)$$

271 where O indicates whether an animal was observed ($O = 1$) or not ($O = 0$), and the
 272 species-level indices are omitted for readability, but each term in the model can be as-
 273 sumed to be species-specific. Smooth effects of percent forest cover (`forest_perc`), eleva-
 274 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

Across species, approximately 10% of GPS fixes had absolute temperatures above 20°C. Of the fixes with finite speed estimates, 2.6% had temperatures lower than -20°C, while 6.5% had temperatures above 20°C, but 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			

301 Across all species, Relative Selection Strength (RSS) was weakest for forest cover and
 302 strongest for elevation. At temperatures near 0°C , boreal caribou selected for forest cover
 303 between 50% and 75%, elevations near 500 m above sea level, and distances from water <
 304 10 km, while southern mountain caribou selected for dense forest cover, elevations near 2
 305 km, and distances from water $\lesssim 5$ km. Cougars selected for dense forest cover ($> 75\%$),
 306 an elevation of ~ 1 km, and distances from water < 7.5 km. Elk selected for intermediate
 307 forest cover ($\approx 50\%$), elevations between 1 and 2 km, and distances from water of 10-15 km.
 308 Grizzly bears selected for relatively sparse forest cover (25-50%), elevation between 1 and 2
 309 km, and distances from water < 3 km. Mountain goats selected for sparse forest cover ($<$
 310 25%), elevations near 1.8 km, and distances from water < 5 km. Finally, wolves selected
 311 for forest cover ($\gtrapprox 50\%$), elevations near 1 km, and distances from water < 5 km. There was
 312 relatively strong agreement between models with and without temperature (Figs. B3, and
 313 B14), but including temperature always resulted in better fits (all p-values $< 2.2 \times 10^{-16}$; all
 314 $\Delta\text{AIC} \geq 342$; Appendix B). Accounting for temperature even resulted in a simpler HRSF

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

318 **3.1 Effects of temperature on movement rates**

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

333 **3.2 Effects of temperature on habitat selection**

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

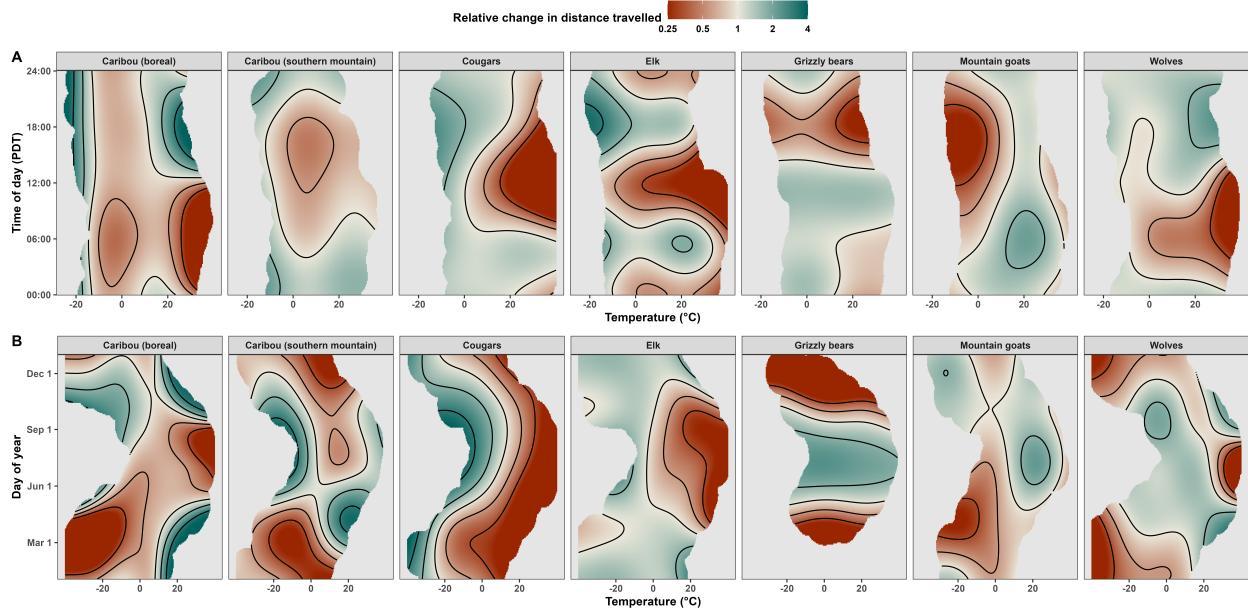


Figure 3: Temperature is a strong driver of how far and when mammals travel. The fill indicates the effects of temperature on the relative change in hourly distance travelled (probability of moving times mean speed when moving) over time of day on June 1st (**A**) and day of year at 12:00 PDT (**B**). Predictions in the surface plots extend to 10% of the range away from each datum to avoid predicting for parameter spaces with no data (grey fill). 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. Horizontal contour lines indicate that movement rates depend most on time of day and day of year (e.g., grizzly bears), while vertical lines indicate that temperature has the greatest effect, irrespective of time (e.g., mountain goats).

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).

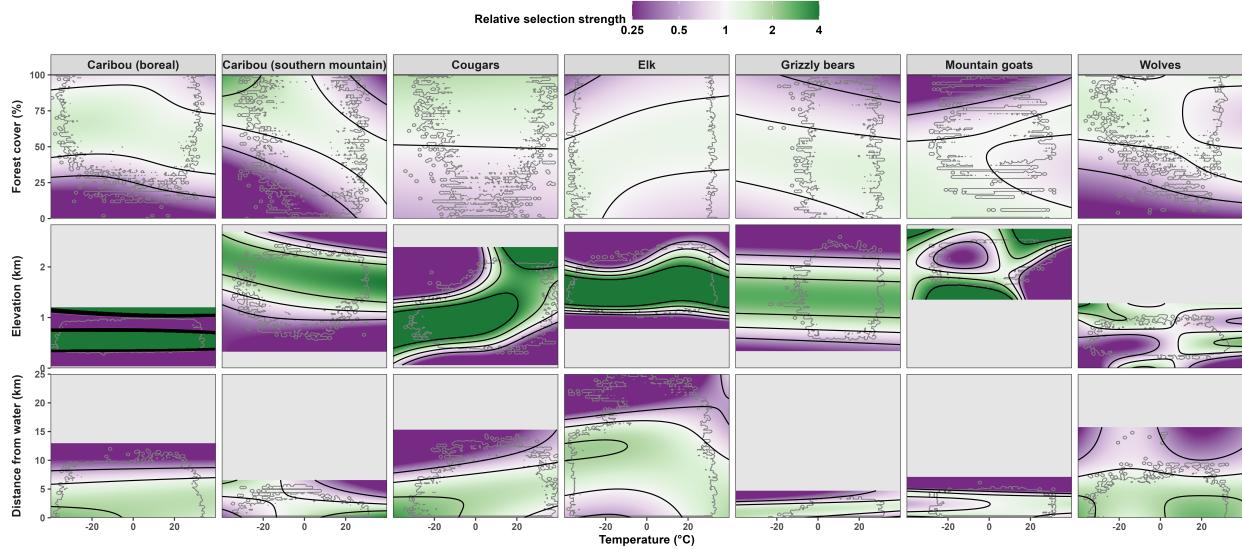


Figure 4: Mammals' habitat selection depends on ambient temperature. Estimated relative selection strength (RSS) for forest cover (%), elevation (km), and distance from water (km) as a function of temperature. The grey contours indicate the extent of each species' observed data. To mitigate the sampling bias across temperature (e.g., grizzly bears have few to no while hibernating in winter), RSS values at each temperature were divided by the average RSS value at that temperature within the respective panel. To further improve readability, each panel's RSS values were centered by dividing by the median RSS value at 0°C and capped to between 0.25 and 4 ($2^{\pm 2}$).

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 higher than at -20°C, independent of changes in the species' movement rates (Fig. 5C-D).

3.3 Predicted changes in movement behaviour during the 21st century

Predicted changes in movement rates with future climate change varied across species in both magnitude and direction, but worse SSPs always corresponded to greater absolute changes (Fig. 6). Additionally, species that were predicted to move less often did not necessarily have lower speeds when moving, and vice versa (Figs. B9 and B10). Estimated changes in average yearly distance traveled were negligible for boreal caribou and grizzly bears, although both species showed seasonal changes in seasonal movement rates. As temperatures warmed,

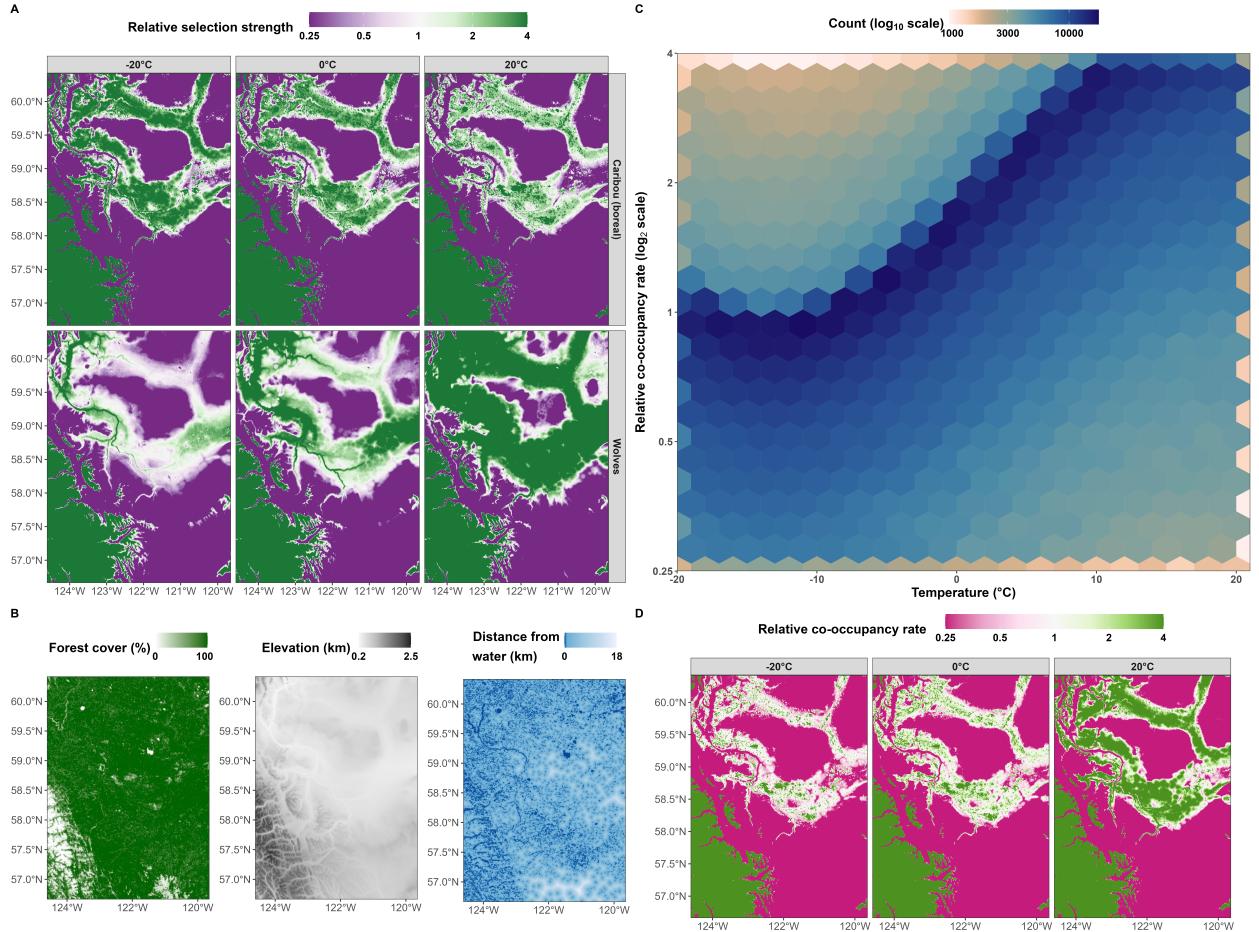


Figure 5: Temperature affects boreal caribou's and wolves' habitat selection and, consequently, their encounter rates. Panel (A) shows the relative selection strength (RSS) for boreal caribou and wolves, as a function of temperature. RSS values were re-centered and capped to between 0.25 and 4 ($2^{\pm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

³⁶⁶ boreal caribou were predicted to move more in winter, spring, and fall but less in summer
³⁶⁷ (Fig. 3), while grizzly bears were predicted to showed a clear shift towards earlier emergence
³⁶⁸ from hibernation (Fig. B4) and greater movement earlier in the year but less movement in
³⁶⁹ early fall. Southern mountain caribou and mountain goats are projected to travel further by
³⁷⁰ 2100, although the estimates for southern mountain caribou varied greatly over space (Fig.
³⁷¹ 7). Cougars, elk, and wolves were projected to move less by 2100, with cougars showing as
³⁷² much as a 24% decrease in mean yearly distance travelled.

³⁷³ Absolute relative changes in predicted yearly distance travelled were small under the
³⁷⁴ best-case SSP (0-4% change in 2100 relative to 2025). Under the worst-case SSP, absolute
³⁷⁵ changes by 2100 (relative to 2025) ranged from ~2% (grizzly bears) to ~24% (cougars).
³⁷⁶ Projected changes in 2100 varied spatially due to spatial heterogeneity in climate change
³⁷⁷ projections (Fig. 7). Again, absolute changes were generally greatest under worse SSPs, but
³⁷⁸ the direction of change at each location also varied across SSPs (most visible in cougars).

³⁷⁹ Median RSS was projected to decrease over time within each species' observed range, but,
³⁸⁰ again, changes were stronger under worse SSPs (Fig. 8). Decreases were most pronounced
³⁸¹ in areas with the lowest RSS and most severe for elk, mountain goats, cougars, and southern
³⁸² mountain caribou. Changes for boreal wolves and caribou were negligible. Elk, cougars,
³⁸³ and grizzly bears were predicted to increase their selection strength for top-RSS areas, and
³⁸⁴ elk, mountain goats, cougars, and southern mountain caribou were predicted to further
³⁸⁵ decrease their selection for areas with low RSS. Unsurprisingly, the predicted change in
³⁸⁶ RSS between 2025 and 2100 also varied spatially for all species (Fig. 9). Overall, RSS
³⁸⁷ decreased throughout most of each species' current range, although elk, cougars, and bears
³⁸⁸ were predicted to increase their selection for higher-altitude habitats. Still, none of the
³⁸⁹ species were projected to increase RSS throughout their habitat (10).

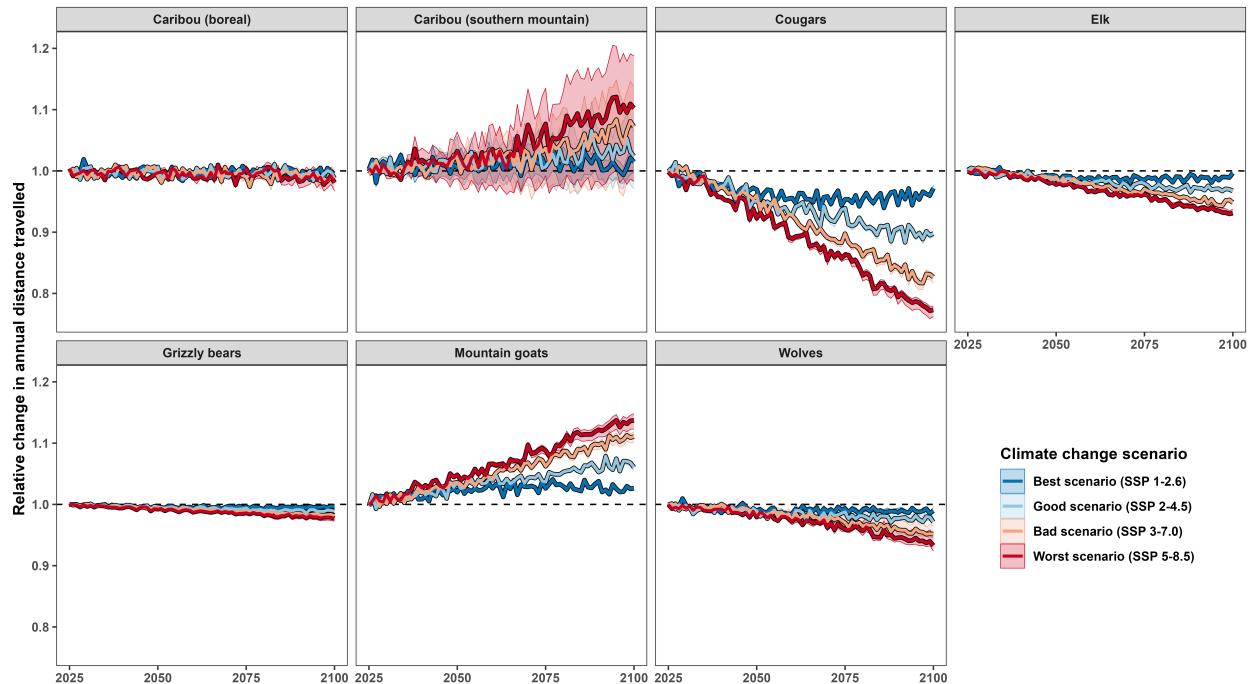


Figure 6: Species are predicted to alter their movement rates differently in response to climate change, and worse climate-change scenarios will result in the greatest change. Bold lines indicate the median change in yearly distance travelled (probability of moving times speed when moving) due to predicted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

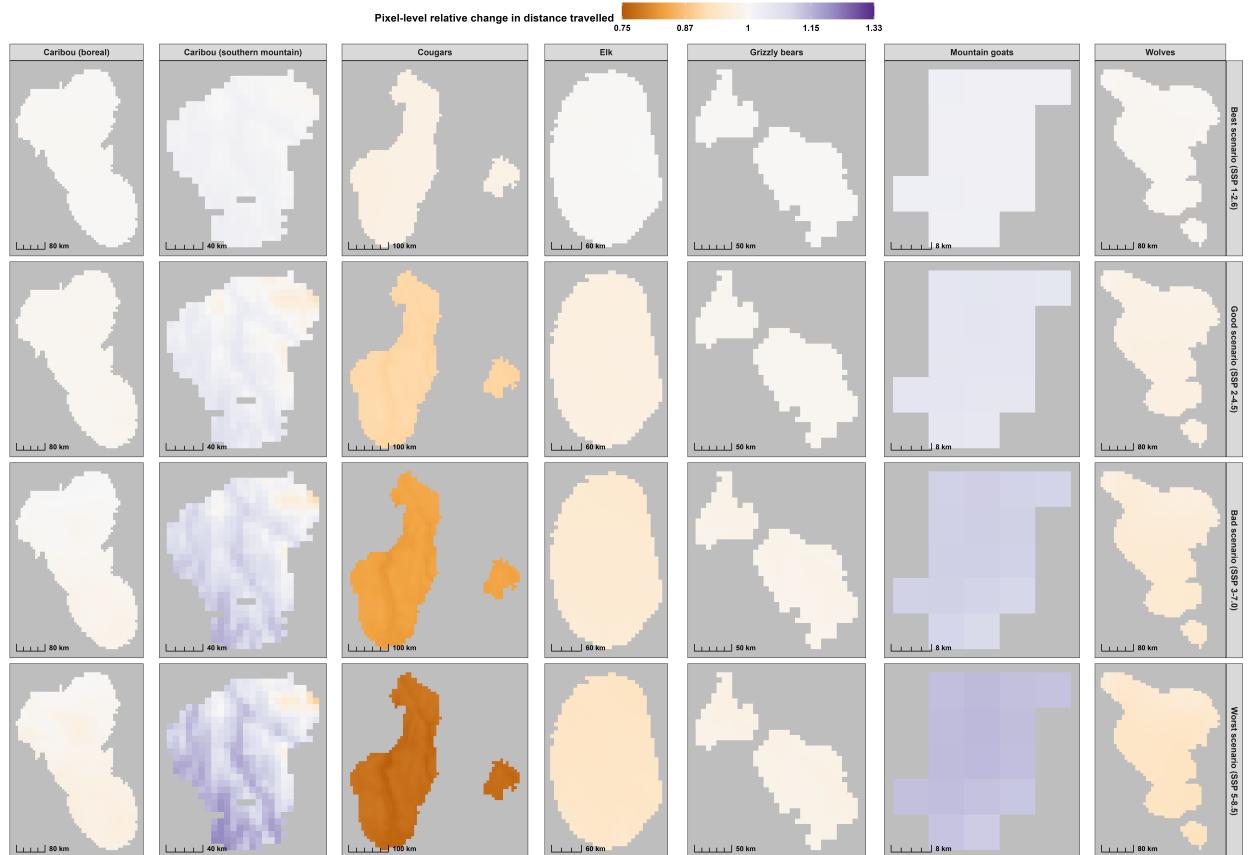


Figure 7: Climate change is predicted to impact each species' movement rates differently, but changes will also vary spatially. The color of each pixel indicates the predicted changes in distance traveled in 2100 at that pixel, relative to the value in 2025, averaged across all four scenarios. Values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

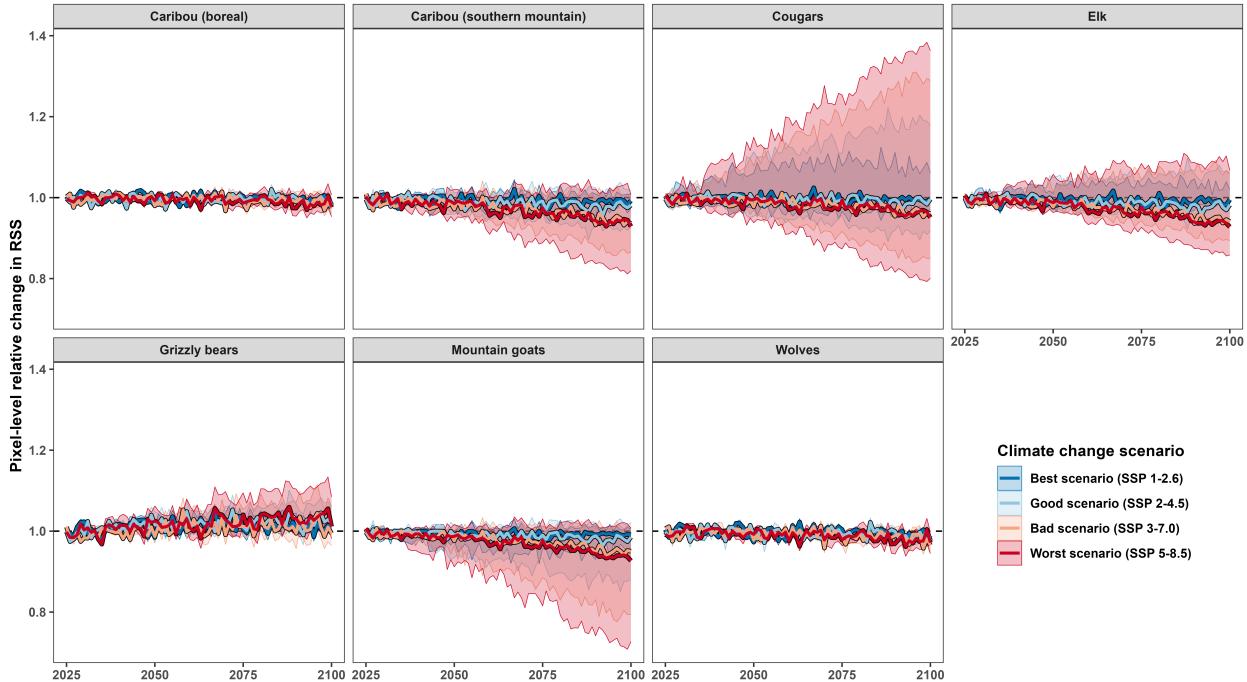


Figure 8: Species are predicted to alter their habitat selection differently in response to climate change, and worse climate-change scenarios will result in the greatest change. Bold lines indicate the change in median RSS due to predicted changes in temperature within each species' study area. Shaded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

390 4 Discussion

391 We have demonstrated that temperature is an important driver of how and where large bo-
 392 real mammals move, and that it affects mammals' seasonal and daily movement behaviour
 393 in complex and nonlinear ways. However, predicting mammals' responses to climate change
 394 remains a challenge, as habitats are warming rapidly and mammals are exposed to increas-
 395 ingly novel and extreme conditions (Diffenbaugh & Field, 2013; Botero *et al.*, 2015; IPCC,
 396 2023). We leveraged the flexibility and interpretability of HGAMs to estimate mammals'
 397 nonlinear responses to temperature without imposing rigid assumptions about the shape of
 398 the responses (Simpson, 2018, 2025). In particular, tensor product interaction terms were
 399 crucial for estimating smooth, nonlinear changes in daily and seasonal trends with tem-
 400 perature with data from multiple individuals. By allowing interaction terms to be smooth
 401 bivariate functions, we were able to quantify changes in movement behaviour without the



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).

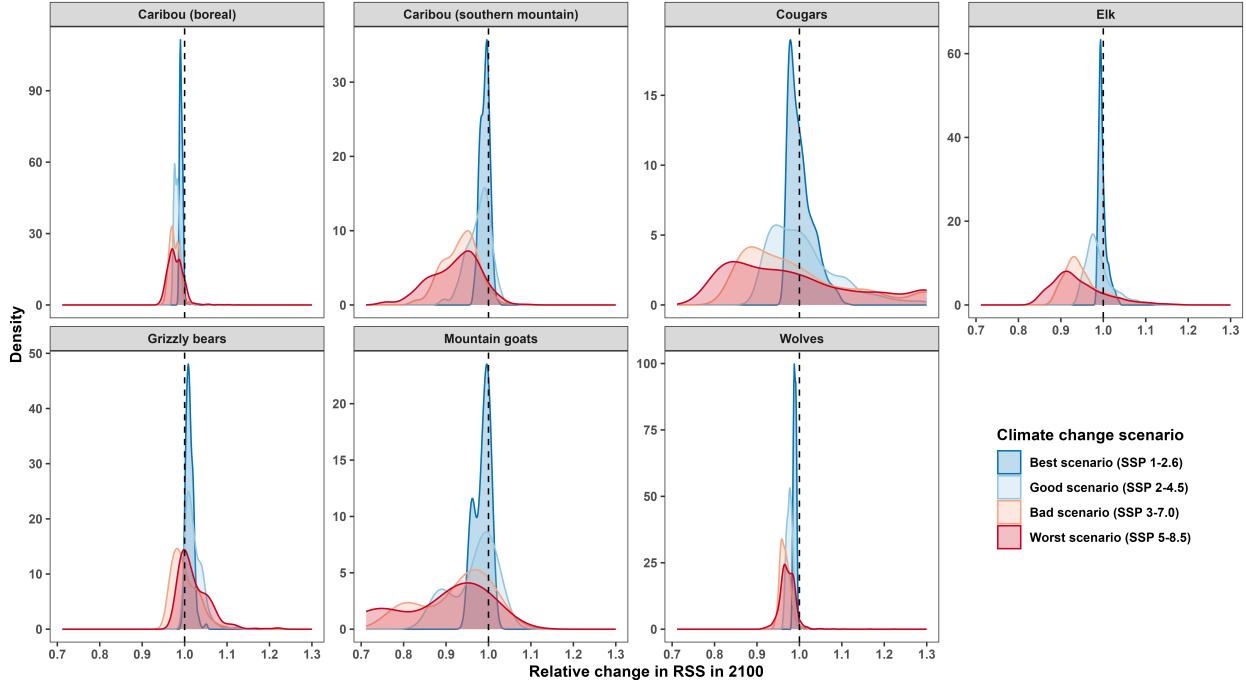


Figure 10: Climate change is predicted to cause species to decrease their selection strength for their current habitats, and worse climate change scenarios will have the greatest impact. The density plots indicate each species’ change in RSS in 2100 for their current habitat (Fig. 8), relative to each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

402 need to discretize time into windows (e.g., day/night and seasons). We were thus able to
 403 present results using relatively simple and interpretable surface plots (Figs. 3 and 4) that
 404 conveyed nuanced, continuous-time estimates of change. This framework was essential for
 405 estimating how mammals behave at extreme temperatures. In fact, despite the recent in-
 406 crease in frequency of extreme heat events in western Canada, including a severe heat wave
 407 in 2021 (Kienzle, 2018; Thompson *et al.*, 2022; Zhang *et al.*, 2023), such events remain rela-
 408 tively rare, so estimating mammals’ nonlinear responses required the flexibility provided by
 409 HGAMs (Wood, 2017). Additionally, the hierarchical approach allowed us to leverage data
 410 from multiple individuals in a single model while accounting for differences in behaviour and
 411 data availability across individuals (Pedersen *et al.*, 2019; Muff *et al.*, 2020; McCabe *et al.*,
 412 2021; Jeltsch *et al.*, 2025; Silva *et al.*, 2025). Still, GAMs’ flexibility and complexity can be a
 413 frustrating limitation if used too generously, so we suggest choosing each smooth term’s basis
 414 size (k) carefully and confirming that estimated responses align with the species’ ecology.

415 While penalized splines and REML can help avoid unruly smooth terms, the penalty terms
416 can struggle to restrict model complexity when datasets are as large as those presented here
417 (Wood, 2017; Wood *et al.*, 2017), so estimated responses should be aligned with biological
418 relevance rather than statistical significance.

419 The effects of warming temperatures on movement rates varied across species, seasons,
420 and space due to differences in species' behavior and physiology as well as their habitats'
421 phenology (e.g., the timing of green-up). For boreal caribou, hotter temperatures decreased
422 movement rates summer but increased them otherwise, mirroring previous studies (Stien
423 *et al.*, 2012; Leclerc *et al.*, 2021; Lessard *et al.*, 2025). The increase in movement rates
424 with temperature during the cold months is likely partly due to shallower snow depth,
425 which results in greater mobility (Pedersen *et al.*, 2021), but warmer temperatures during
426 snowy seasons also increase the risk of temperature fluctuations near 0°C and the risk of
427 rain-on-snow events (Musselman *et al.*, 2018), which limit forage availability and increase
428 time spent foraging (Stien *et al.*, 2012; Berger *et al.*, 2018; Mezzini *et al.*, 2025). The
429 reduced movement rates during warmer summers are likely mainly due to more frequent
430 resting and use of thermal refugia, given ungulates' documented risk of hyperthermia (Alston
431 *et al.*, 2020; Verzuh *et al.*, 2023). Therefore, although we predict that boreal caribou's
432 yearly average movement rates will remain approximately unchanged throughout the 21st
433 century, the projections do not show the changes in seasonal movement phenology. This is an
434 important caveat, since the effects of extreme temperatures are exacerbated by phenological
435 mismatches with seasonal photoperiod (Walker *et al.*, 2019), including the timing of molting
436 and reproduction. Earlier growth seasons in boreal and arctic regions have resulted in lower
437 calf birth and survival (Post & Forchhammer, 2008), while the lengthening of the growth
438 season has allowed moose (*Alces alces*) and deer to encroach on boreal caribou habitat and
439 increase the density of coyotes (*Canis latrans*), cougars, and wolves (Barber *et al.*, 2018;
440 DeMars *et al.*, 2023), whose movement behaviour also depends on ambient temperature.

441 Boreal wolves responded to temperature similarly to boreal caribou, and habitat selection

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

Considerations about changes in trophic interactions leads to another important caveat about the results we present. The estimated changes in movement behaviour cannot be fully attributed to physiological responses to temperature alone, since other aspects of habitats' seasonal phenology are (nonlinearly) correlated with temperature. For example, mountain goats' lower movement rates at temperatures near 0°C in winter may be due to a multitude of factors, including: increased movement difficulty, since melting snow and rain-on-snow events increase the energetic costs of movement (White, 2025); reduced movement during

469 storms (Musselman *et al.*, 2018); and increased encounter risk with predators (Sullender
470 *et al.*, 2023). However, milder temperatures can also increase plant growth, which allows
471 goats to spend more time foraging within and less time travelling across patches (Charnov,
472 1976; White *et al.*, 2025). Therefore, Fig. 3 illustrates an estimate of the total effects of
473 temperature on each species' movement rates, but it does not explicitly account for energetic
474 costs. Similarly, species' changes in habitat selection do not explicitly account for any changes
475 in physiological or energetic costs. Additionally, forest cover, elevation, and distance from
476 water are often correlated, so the estimated effects should be interpreted carefully, and they
477 may not be applicable outside the study areas used here. For example, both mountain goats
478 and elk selected for higher elevation as temperatures warmed, but our models did not account
479 for differences in forage availability at different elevations.

480 Climate change has also had extensive impacts on plant growth and phenology (Cleland
481 *et al.*, 2007; Denny, 2019; Tysor, 2025) with consequences on herbivores' behaviour and fit-
482 ness (Post & Forchhammer, 2008; Aikens *et al.*, 2017). Plants' limited ability to disperse to
483 and establish in new habitats is often a limiting factor for herbivores' ability to escape hotter
484 temperatures by moving to higher altitudes or latitudes, and the advance of herbivores can
485 further limit plants' ability to establish (Speed *et al.*, 2012; Diffenbaugh & Field, 2013).
486 Consequently, mammals that move to higher elevations may be forced to spend more time
487 foraging if forage is scarce or unpredictable (Mezzini *et al.*, 2025), which will increase both
488 their energetic expenditure and encounter rates with predators and competitors (Kohl *et al.*,
489 2019; Martinez-Garcia *et al.*, 2020; Tórrez-Herrera *et al.*, 2020; Smith *et al.*, 2023). If local
490 high-elevation habitats become unsuitable, and moving to nearby higher peaks requires trav-
491 eling across low-quality and high-risk habitat (Fig. 9), habitat fragmentation may prevent
492 movement between ranges (White *et al.*, 2025). Consequently, proactive corridor planning
493 will be crucial in allowing species to mitigate the effects of climate change, and corridors
494 should include a wide range of habitat (Sawyer *et al.*, 2009; Stralberg *et al.*, 2020; Morley,
495 2021).

496 Growing evidence suggests that mammals' exposure, sensitivity, and adaptability to cli-
497 mate change will limit their ability to adapt to change (Ameca y Juárez *et al.*, 2012; Diffen-
498 baugh & Field, 2013). Exposure to warming temperatures is widespread throughout western
499 Canada (Bunnell *et al.*, 2011; Kienzle, 2018; Eum *et al.*, 2023), and changes in temperature
500 and phenology may be too rapid for many species to respond to (Diffenbaugh & Field, 2013).
501 Species' adaptability is further challenged by the difficulty in responding to concurrent, mul-
502 tifarious, and interconnected changes (Polazzo *et al.*, 2024), including changes in: climate,
503 land and sea use, direct exploitation of organisms, pollution, and invasion of alien species
504 (Diffenbaugh & Field, 2013; IPBES *et al.*, 2019). In the future, landscapes may thus become
505 unable to support species and population sizes they supported historically, and species may
506 begin selecting against historical ranges (Williams & Blois, 2018). Therefore, it is crucial
507 for conservationists to distinguish between a species' ideal environmental space and its best
508 available geographic space (*sensu* Matthiopoulos, 2022).

509 Accelerating multifarious change in species' movement behaviour and energetic costs re-
510 quire conservation measures that are proactive and anticipate future changes. Polazzo *et al.*
511 (2024) present a framework for estimating species' responses to multifarious change using
512 GAMs that is particularly useful when estimating species' (nonlinear) responses to inter-
513 actions between environmental variables (e.g., changes in both temperature and limiting
514 nutrients). By accounting for the effects of multiple variables at once, they demonstrate
515 how a species' response to one variable can depend on other concurrent changes. Estimat-
516 ing responses to multifarious change is crucial in assessing mammals' responses to hotter
517 temperatures, altered phenology, and novel community dynamics. For instance, warming
518 temperatures have increased exposure to disease and parasites, with impacts on mammalian
519 physiology and energetic needs (Pickles *et al.*, 2013; Barber *et al.*, 2018; Blanchong *et al.*,
520 2018; Gray & Ogden, 2021; Gude *et al.*, 2022). In particular, severe tick loads can reduce
521 mammals' ability to thermoregulate in the cold due to reduced body fat and fur (Pekins,
522 2020) and can even reduce movement rates by increasing time spent recumbent (Addison *et*

523 *al.*, 2023).

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

533 Future work should develop models that account for covariates that are specific to the
534 study species and area, such as forest age and disturbance (DeMars *et al.*, 2023), terrain
535 ruggedness (White & Gregovich, 2017), anthropogenic linear features (Dickie *et al.*, 2017),
536 greater physiological stress from infection and parasitism (Pickles *et al.*, 2013; Gude *et al.*,
537 2022), and growing human presence in wild spaces (Sih *et al.*, 2011; Rice, 2022), including
538 the growing risk of human-wildlife conflict (Abrahms *et al.*, 2023; Weststrate *et al.*, 2024). In
539 particular, forests in western Canada are highly dynamic over time (Zhang *et al.*, 2015), and
540 fires size and burn severity have increased in western Canada in recent decades (Whitman *et*
541 *al.*, 2022; Parisien *et al.*, 2023; Wang *et al.*, 2025). Thus, while our use of a static raster of
542 forest cover allowed for simpler models and climate change projections, future studies should
543 account for mammals' responses to temporal forest dynamics, including the impacts of fire
544 (Whitman *et al.*, 2022; Parisien *et al.*, 2023; Wang *et al.*, 2025), logging (Lochhead *et al.*,
545 2022) and other extractive industries (Dickie *et al.*, 2017, 2024). Additionally, rising inci-
546 dence of disease and parasite load over the coming decades may also alter increase mammals'
547 energetic needs (Gude *et al.*, 2022) and time spent foraging or hunting (Mezzini *et al.*, 2025).
548 However, the inclusion of temporally dynamic variables will require that any future projec-
549 tions of species' behaviour depend on temporally dynamic estimates of how such variables

550 will change over the years.

551 We have demonstrated that temperature has complex and nonlinear effects on how and
552 where mammals move. Rising temperatures have impacted mammals' daily and seasonal
553 movement cycles, and changes are expected to intensify throughout the 21st century. Quan-
554 tifying how temperature affects mammalian behavior and fitness is a first step towards
555 developing an understanding of the effects of climate change on landscape dynamics and the
556 effectiveness of protected areas in the future. By leveraging the flexibility and statistical
557 power of Hierarchical Generalized Additive Models, we have provided researchers with mal-
558 leable and data-driven methods for assessing species' responses to climate change. We hope
559 that future work will develop more species-specific models with the intent of developing a
560 community-level framework for quantifying and predicting how communities will respond to
561 climate change.

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567 Author contributions

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

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