

Rising temperatures alter how and where mammals move

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

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

Kirk Safford⁶ Robert Serrouya^{1,2,7} Michael J. Noonan^{1,2,8}

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 British Columbia Ministry of Environment and Parks, Penticton, BC, Canada.

⁷ Wildlife Science Centre, Biodiversity Pathways, University of British Columbia Okanagan, Revelstoke, British Columbia, Canada.

⁸ Department of Computer Science, Math, Physics, and Statistics, The University of British Columbia Okanagan, Kelowna, British Columbia, Canada.

Running Title: Temperature alters mammal movement behavior

Article type: Research article

Words in abstract: 300

Words in main text: 7533

Figures: 9

Tables: 3

References: 147 (updated on 2025-09-30)

Appendices: 2

Key words: climate change, temperature, mammals, animal movement, movement behaviour, habitat selection, projections

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 uncertain how mammals will adapt their movement behaviour throughout the 21st century. We address this gap by quantifying the effects of temperature on the movement rates and habitat selection of six large-bodied mammalian species (boreal and southern mountain caribou, cougars, elk, grizzly bears, mountain goats, and wolves) throughout western Canada between 1998 and 2023. We show that temperature significantly affected of how and where these mammals moved, and we predict that climate change will impact mammals' movement behaviour throughout the 21st century, although species did not respond uniformly to temperature. Projected responses to climate change suggested that rising temperatures will drive southern mountain caribou and mountain goats to move more, while cougars, elk, and wolves will move less. Boreal caribou and grizzly bears showed little change in projected yearly movement rates but clear shifts in seasonal phenology. We also predict that rising temperatures will reduce median habitat selection strength most of the six species, but some are expected to show increased selection strength for higher altitudes. As mammals increasingly alter their movement rates and select against portions of their current ranges, changes in individuals' movement behaviour will impact encounter rates, including predator-prey dynamics and human-wildlife interactions. Conservation efforts should therefore account for future changes in movement behaviour as well as the consequences such changes may have on communities. Proactively anticipating changes in mammalian movement behaviour will become crucial for effectively and proactively understanding community-level responses and selecting high-quality habitat for long-term conservation.

¹ 1 Introduction

² For most animals, movement is a rapid and low-cost response to a variety of stimuli (Nathan
³ *et al.*, 2008). Animals move to optimize resource use (e.g., food, water, shelter; Charnov,
⁴ 1976; Kacelnik *et al.*, 1992; Merkle *et al.*, 2016; Mezzini *et al.*, 2025), optimize habitat use
⁵ (Winter *et al.*, 2024), and avoid predators and competitors (Tórrez-Herrera *et al.*, 2020; Pe-
⁶ terson *et al.*, 2021; Bartashevich *et al.*, 2024; Tan *et al.*, 2024). How and where animals move
⁷ thus also determines encounter rates with resources (Mezzini *et al.*, 2025), humans (Johnson
⁸ *et al.*, 2018; Weststrate *et al.*, 2024), predators, prey, and competitors (Martinez-Garcia *et*
⁹ *al.*, 2020; Glass *et al.*, 2021; Brivio *et al.*, 2024). However, ambient temperature affects
¹⁰ animals' movement rates by altering the energetic cost of movement and thermoregulation
¹¹ (McNab, 1970; Taylor *et al.*, 1982; Brown *et al.*, 2004; Fuller *et al.*, 2016; Jahn & Seebacher,
¹² 2022), and extreme temperatures can impact animals' movement rates (Dyer *et al.*, 2023),
¹³ phenology (McLellan & McLellan, 2015; Pigeon *et al.*, 2016; Johnson *et al.*, 2018; Carbeck *et*
¹⁴ *al.*, 2022), and life history (Newediuk *et al.*, 2024), and even cause physiological damage and
¹⁵ death (Heten *et al.*, 2014; Powers *et al.*, 2017; Ratnayake *et al.*, 2019; Schmidt *et al.*, 2020;
¹⁶ Schwerdt *et al.*, 2024). Animals may search for a short-term buffer from extreme tempera-
¹⁷ tures by moving to thermal refugia (Hannah *et al.*, 2014; Elmore *et al.*, 2017; Attias *et al.*,
¹⁸ 2018; Arechavala-Lopez *et al.*, 2019; Gulland *et al.*, 2022), and shelter may even be preferred
¹⁹ over forage abundance (Hall *et al.*, 2016). However, climate change during the last century
²⁰ (IPCC, 2023) have caused animals to alter how and where they move as they respond to
²¹ hotter temperatures and increasingly severe and frequent extreme-heat events (Bunnell *et*
²² *al.*, 2011; IPCC, 2023).

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

27 damage in a shorter span of time (Jessen, 2001; Sherwood & Huber, 2010; Mota-Rojas *et*
28 *al.*, 2021; Newediuk *et al.*, 2024). Mammals' homeothermy can cause them to have difficulty
29 dissipating heat, particularly when ambient temperatures are near or above body tempera-
30 ture. Large-bodied mammals are most likely to alter their movement behaviour with rising
31 temperatures, since they tend to move long distances (Merkle *et al.*, 2016), are particularly
32 sensitive to overheating (Fuller *et al.*, 2016; Alston *et al.*, 2020; Verzuh *et al.*, 2023), and
33 their movement rates are thus strongly limited by excessive heat (Dyer *et al.*, 2023). Global
34 warming during the last century has resulted in milder and shorter winters, hotter and longer
35 summers, and a greater risk of extreme-heat events (IPCC, 2023), with widespread changes
36 in mammals' seasonal phenology, fitness, and life history (Botero *et al.*, 2015; McLellan &
37 McLellan, 2015; Pigeon *et al.*, 2016; Wells *et al.*, 2022; Newediuk *et al.*, 2024). However, be-
38 havioral responses to heat vary substantially across species depending on body size, vagility,
39 and activity times (McCain & King, 2014; Williams & Blois, 2018). For example, warming
40 temperatures have allowed deer (*Odocoileus* spp.) to shift northward, which has led to in-
41 creased density of wolves (*Canis lupus*) and higher predation on caribou (*Rangifer tarandus*
42 *caribou*) (Latham *et al.*, 2011; Barber *et al.*, 2018; Dickie *et al.*, 2024). Preparing for and
43 responding to future changes will require a detailed understanding of not only how and where
44 mammals move throughout the thermal landscape but also the cascade of effects that
45 such changes will have at the population and community levels (Cunningham *et al.*, 2021).

46 As heat stress intensifies over the next 100 years, mammals will continue to suffer impacts
47 on their fitness, movement rates, and habitat selection (Deb *et al.*, 2020; Woo-Durand *et*
48 *al.*, 2020). It remains unclear how or whether species will be able to respond to climate
49 change in the current century (Deb *et al.*, 2020; Woo-Durand *et al.*, 2020; Verzuh *et al.*,
50 2023), especially if populations fail to adapt (Botero *et al.*, 2015; Sawyer *et al.*, 2019) or are
51 physiologically incapable to do so (Sherwood & Huber, 2010; Botero *et al.*, 2015; Williams
52 & Blois, 2018). Recent work has documented the effects of climate change on mammals'
53 ranges (Leclerc *et al.*, 2021), thermoregulation (Mota-Rojas *et al.*, 2021), and movement

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

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

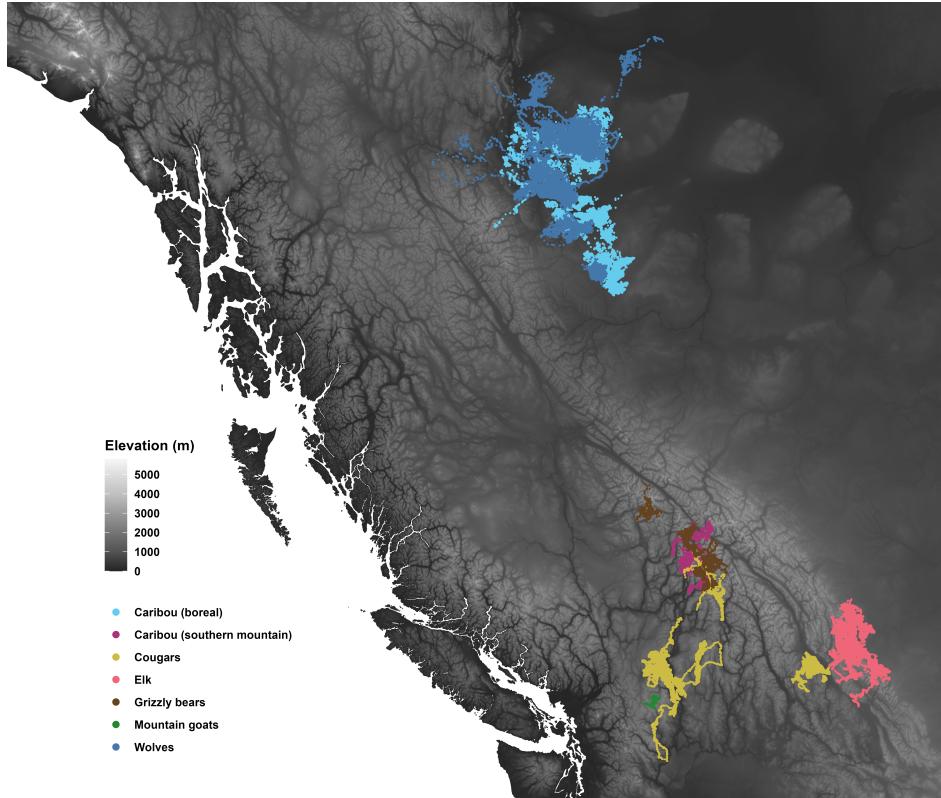


Figure 1: GPS telemetry data for the six species in this study (dots) over a digital elevation model for the study area.

Table 1: Summary statistics of each species' set of GPS data, namely: the start and end of each set of GPS telemetries, the number of GPS fixes (after data cleaning), the number the median sampling interval (Δt ; stratified by animal), the number of animals (Animals), and the number of animals with finite speed estimates (Has speed).

Species	Start	End	n	Δt (hours)	Animals	Has speed
Caribou (boreal)	2011-03-02	2018-01-03	200,561	13.00	146	131
Caribou (southern mountain)	1998-03-20	2009-06-06	27,921	6.00	22	20
Cougars	2006-02-04	2021-07-12	80,650	2.00	29	29
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. See the discussion section for additional
97 detail on the advantages and limitations of using such simple models.

98 **2.1.1 GPS telemetry data**

99 Boreal caribou and wolf telemtries were acquired from a data repository of the British
100 Columbia Oil and Gas Research and Innovation Society (BC ORGIS) that was collected as
101 part of the boreal caribou radio-collaring program of the BC OGRIS Research and Effective-

ness Monitoring Board (REMB; BC OGRIS, 2018). Southern mountain caribou data were obtained from the work of Ford *et al.* (2023). Cougar data include telemetries from Darlington *et al.* (2025) and (*serrouya_ref?*). Elk data from the work of Ciuti *et al.* (2012) were downloaded from Movebank (Kays *et al.*, 2022). ***MISSING INFO ON GRIZZLY BEAR AND GOAT TELEMETRY DATA.***

From the full set of telemetry data, we removed a total of 2396 problematic GPS locations (0.16%, including collar calibration data) after inspecting diagnostic plots of (1) distance from the median location, (2) straight-line displacement between locations, (3) turning angle, and (4) time interval between consecutive points. Particular attention was paid to points with large turning angles ($\gtrapprox 170^\circ$) and excessively high straight-line displacement, especially if antecedent and subsequent points indicated relatively stationary behaviour (Appendix A).

2.1.2 Historical temperature data and climate change projections

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

To obtain projected average monthly temperatures from 2025 to 2100 at a 0.08° spatial resolution, we used the `climatenaR` package (v. 1.0, Burnett, 2023) for R and ClimateNA v. 7.4.2 (Wang *et al.*, 2016; Mahony *et al.*, 2022). However, the climate projections only included estimates of future monthly averages, a scale substantially coarser than that of our tracking data (Table 1). To estimate the distribution of temperatures at an hourly scale within a month, we assumed values to be approximately normally distributed with mean μ_T and variance σ_T^2 . We estimated μ_T using the ClimateNA projections, while we estimated σ_T^2 by modeling the observed variance in historical weather data for western Canada from

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

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

142 where $\mu_{\sigma_T^2}$ and $\nu_{\sigma_T^2}$ indicate the location and scale parameters of the gamma distribution of
 143 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
 144 $f_{S,j}$ indicate the j^{th} smooth functions for the location and scale parameters, respectively.
 145 To ensure the smooth functions of month, $f_{L,2}(m)$ and $f_{S,2}(m)$, joined smoothly between

¹⁴⁶ December and January, the terms use cyclic cubic spline bases. The spatial terms used two-
¹⁴⁷ dimensional Duchon splines, a generalization of thin-plate regression splines (p. 221 of Wood
¹⁴⁸ (2017)). The smoothness parameters were estimated via REstricted Maximum Likelihood
¹⁴⁹ (REML; p. 83 of Wood, 2017). See the Data Availability Statement for additional information
¹⁵⁰ on the code used to fit the model.

¹⁵¹ We simulated hourly variation in future years by assuming hourly temperature followed
¹⁵² a normal distribution with mean specified by the monthly `climatenar` climate projections
¹⁵³ and variance as specified by the gamma GMLS. For each month within each year from
¹⁵⁴ 2025 to 2100, we simulated hourly weather by including temperatures from the 0.1 to the
¹⁵⁵ 0.9 quantiles by increments of 0.1, and we weighted each quantile proportionally to the
¹⁵⁶ (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 ($\text{cover} > 0\%$) or without water ($\text{cover} = 0\%$) and then calculated each pixel's distance from
¹⁶⁴ the nearest pixel with water using the `distance()` function from the `terra` package. Fi-
¹⁶⁵ nally, we obtained two digital elevation models using the `get_elev_raster()` function from
¹⁶⁶ the `elevatr` package (v. 0.99.0, Hollister *et al.*, 2023). We used a raster with a zoom of 6
¹⁶⁷ (a resolution of 0.009°) for model fitting and one with a zoom of 3 (a resolution of 0.08°)
¹⁶⁸ for downloading climate change projections via `climatenar`. All final rasters and code are
¹⁶⁹ available on GitHub (see the Data Availability Statement). For ease of interpretability and
¹⁷⁰ comparison with current conditions, we assumed resources would remain constant through
¹⁷¹ to 2100, although we recognize that the spatial distribution of forest cover and open water

172 will likely change throughout the 21st century.

173 **2.2 Estimating mammals' instantaneous speeds**

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

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

190 **2.3 Estimating the effects of temperature on mammals' movement behaviour**

191 Ambient temperature is only one of the many drivers of mammalian movement behaviour
192 (Fig. 2). Many species alter their movement rates (e.g., movement frequency and speed)
193 daily or seasonally in response to factors such as solar time, photoperiod, forage availability,
194 reproductive cycles, and predator avoidance. Similarly, ambient temperature also fluctuates
195 throughout the day and across seasons. Therefore, estimating the effects of temperature
196 on movement rates requires accounting for how mammals' response to temperature changes

197 with time of day and day of year (Fig. 2A; Péron *et al.*, 2017; Buderman *et al.*, 2018; Leclerc
 198 *et al.*, 2021; Xu *et al.*, 2021). Similarly, mammals' selection strength for resources depends
 199 on ambient temperature, since higher temperatures can promote a selection for refuge from
 200 heat (e.g., thicker forest cover, higher elevation, proximity to water; Attias *et al.*, 2018;
 201 Giroux *et al.*, 2023).

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

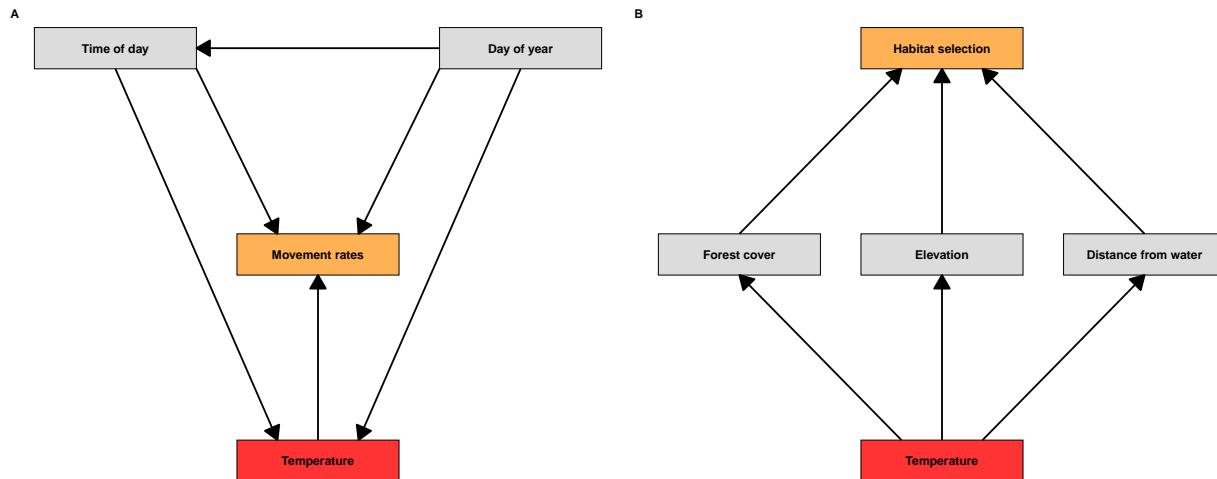


Figure 2: Directed Acyclical Graphs (DAGs) assumed for inferring the causal effects of temperature on each species' movement behaviour. (A) Ambient temperature affects mammals' movement rates (i.e. probability of moving, speed when moving, and distance traveled), but temperature is influenced by time of day and day of year. Additionally, the effects of temperature on movement rates depend on time of day and season, since animals may respond to temperatures differently at different times of day and or days of year. Finally, the effect of time of day changes seasonally due to changes in photoperiod. (B) Similarly, habitat selection depends on the availability and selection of resources (forest cover, elevation, and distance from water), but the selection strength for each resource is conditional on temperature. For example, an animal may avoid forested areas unless it is seeking refuge from extreme temperatures.

207 2.3.1 Effects of temperature on movement rates

208 We estimated the effects of temperature on mammals' instantaneous movement state (mov-
 209 ing or not) and speed when moving using two Hierarchical Generalized Additive Models

(HGAMs; Pedersen *et al.*, 2019 and Appendix B) with the `mgcv` package for R. The first HGAM estimated the probability that an animal was moving, $P(M)$, with a binomial family of distributions and logit link function. The second HGAM estimated an animal's speed when moving with a gamma family of distributions and log link function. We fit the models with fast Restricted Maximum Likelihood ('fREML') and discretized covariates (`discrete = TRUE`) to optimize computational efficiency with no appreciable losses to model performance (Appendix B; Wood *et al.*, 2015, 2017; Li & Wood, 2020). Together, the binomial HGAM and the gamma HGAM inform us on an animal's long-term average speed, since it is the product of the probability of moving and its average speed when moving.

The HGAMs (equations (2) and (3)) included fixed-effect intercepts for each species (β_s), random intercepts for each animal (Z_a), and species-level `by` smooths that allowed independent smoothness parameters for each species (model I in Figure 4 of Pedersen *et al.*, 2019). The `by` smooths accounted for trends in time of day (in Pacific Daylight Time; `tod_pdt`), day of year (`doy`), and temperature (`temp_c`). To account for the cyclicity of time of day and day of year, the smooth terms used cyclic cubic splines (p. 202 of Wood, 2017). The models also had three tensor product interaction terms `by` each species: (1) day of year and time of day, (2) temperature and time of day, and (3) temperature and day of year. These three terms accounted for smooth changes in: (1) daily behaviour across day of year, (2) the response to temperature over time of day (e.g., changes in nocturnality), and (3) the response to temperature over day of year (e.g., the timing of molting, migration, and hibernation). Finally, two smooth terms of log-transformed sampling interval (`dt`; hours) corrected for biases in speed estimates arising from irregular GPS sampling intervals, since longer intervals result in lower speed estimates (Nathan *et al.*, 2022; DeNicola *et al.*, 2025). A global smooth term of $\log(dt)$ accounted for the overall effect of sampling interval, while a factor-smooth interaction term (`bs = 'fs'`) of $\log(dt)$ and species accounted for species-level deviations from the global term while assuming a common smoothness parameter across species (model GS in Figure 4 of Pedersen *et al.*, 2019). Formally, the model for movement

²³⁷ state M , with $M = 0$ indicating no movement and $M = 1$ indicating movement, was

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

²³⁸ while the model for movement speed when moving (i.e., $M = 1$, indicated with S) was

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

²³⁹ In both models, β_s indicates a fixed intercept for species s , Z_a indicates a Gaussian random
²⁴⁰ effect for animal a (of species s), $f_{j,s}$ indicates the j^{th} smooth function for species s , and
²⁴¹ functions with two variables indicate tensor product interaction terms. The model code used
²⁴² to fit the models is available in Appendix B.

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

²⁴⁴ We estimated the effects of temperature on each species' selection for percent forest
²⁴⁵ cover (`forest_perc`), elevation (`elevation_m`, in meters), and distance from water
²⁴⁶ (`dist_water_m`, in meters) by fitting a Hierarchical Resource Selection Function (HRSF) for
²⁴⁷ each species (McCabe *et al.*, 2021). We fit each HRSF using an HGAM with a Poisson family
²⁴⁸ of distributions and log link function (Appendix B; Aarts *et al.*, 2008). After removing
²⁴⁹ non-resident individuals (Table B1), we accounted for the spatiotemporal autocorrelation
²⁵⁰ in the telemetry locations by weighting each point based on the telemetry's Autocorrelated
²⁵¹ Kernel Density Estimate (Fleming & Calabrese, 2017; Noonan *et al.*, 2019b; Alston *et al.*,
²⁵² 2022) to produce estimates of second-order habitat selection (Johnson, 1980). Quadrature
²⁵³ points were used to approximate the likelihood function of a Poisson point process through
²⁵⁴ Monte-Carlo Markov chain-based integration (Aarts *et al.*, 2008; Fithian & Hastie, 2013;
²⁵⁵ Baddeley *et al.*, 2015) and were determined using the raster cells in each animal's 99.9%
²⁵⁶ AKDE percentile, with each raster cell having a weight of 1. The number of quadrature
²⁵⁷ locations greatly outnumbered the number of observed locations (Fig. B12), especially after
²⁵⁸ accounting for the AKDE weights (Fig. B13).

²⁵⁹ Each species' model had the same structure:

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

²⁶⁰ where O indicates whether an animal was observed ($O = 1$) or not ($O = 0$), and the

species-level indices are omitted for readability, but each term in the model can be assumed to be species-specific. Smooth effects of percent forest cover (`forest_perc`), elevation (`elevation_m`, in meters), and distance to water (`dist_water_m`, in meters) accounted for the species-level selection strength for each resource. A Gaussian random effect for each individual animal (Z_a) corrected for uneven sampling across individuals, while factor-smooth interaction terms for each animal ($f_{j,a}$) accounted for animal-level resource selection (i.e., individual-level deviations from the species-level estimate; Jeltsch *et al.*, 2025). Tensor product interaction terms of the three resources and temperature (`temp_c`) estimated the smooth change in resource selection at different temperatures. Finally, marginal smooth terms of temperature and factor-smooth interaction terms of temperature and animal accounted for species- and individual-level sampling biases at different temperatures (e.g., sampling more during warm periods).

3 Results

Of the GPS fixes with finite speed estimates, 2.6% had temperatures lower than -20°C , while 6.5% had temperatures above 20°C , and temperature ranges differed across species (Table 2, Fig. B2). Sampling interval affected estimates of probability as well of as speed when moving (Fig. B8). 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: $0.42 - 2.67 \text{ km/h}$), and mean distance traveled (i.e., $\hat{P}(M) \times \hat{\mathbb{E}}(S|M = 1)$, range: $0.04 - 0.61 \text{ km/h}$; 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 ($\hat{\mathbb{E}}(S|M = 1) \approx 0.43 \text{ km/h}$), while wolves had the highest mean speed when moving ($\hat{\mathbb{E}}(S|M = 1) \approx 2.67 \text{ km/h}$). Consequently, at 0°C , wolves traveled an average of $0.22 \times 2.67 \text{ km/h} \approx 0.6 \text{ km/h}$; 2.5 to 16.7 times further than other species.

Table 2: Summary statistics for each species' GPS fixes with finite speed estimates, namely: the number fixes after data cleaning (n), the percentage of fixes with temperature (T) below -20°C and above 20°C , the estimated mean probability of moving ($\hat{P}(M = 1)$), the mean speed when moving ($\hat{\mathbb{E}}(S|M = 1)$; km/h), and the mean distance travelled ($\hat{P}(M = 1) \times \hat{\mathbb{E}}(S|M = 1) = \hat{\mathbb{E}}(D)$; km/h), for a sampling interval of 1 hour and a temperature T of 0°C .

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

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

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

303 produced a better fit.

304 **3.1 Effects of temperature on movement rates**

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

321 **3.2 Effects of temperature on habitat selection**

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

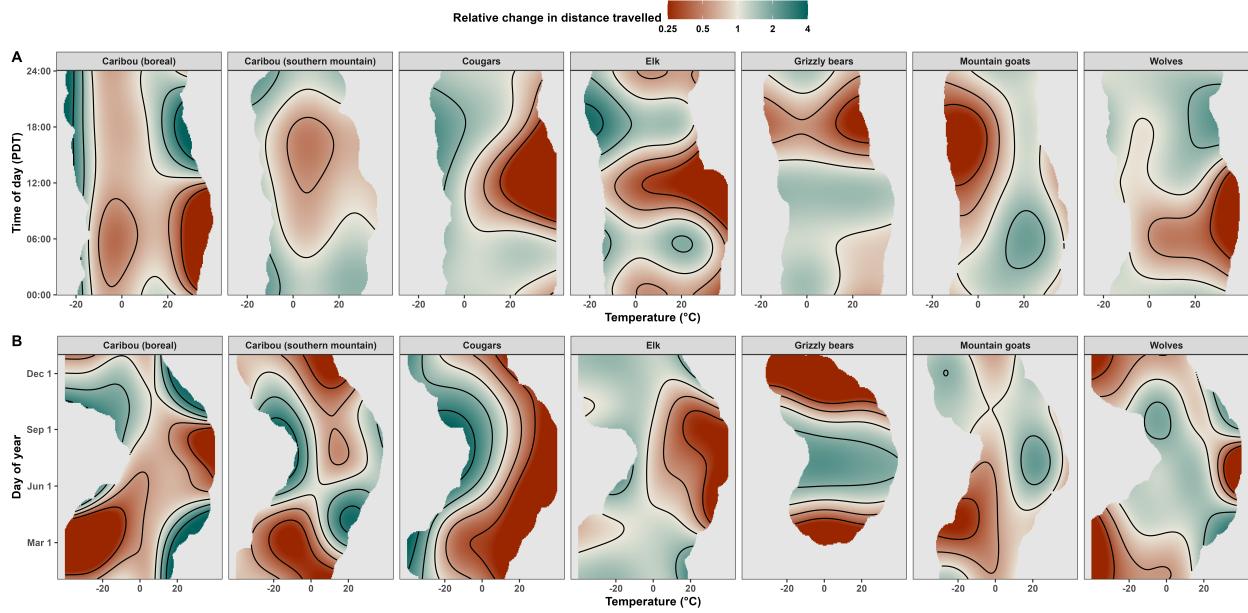


Figure 3: Temperature is a strong driver of how far and when mammals travel. The fill indicates the effects of temperature on the relative change in distance travelled (probability of moving times mean speed when moving) over time of day on June 1st (**A**) and day of year at 12:00 PDT (**B**). Predictions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

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

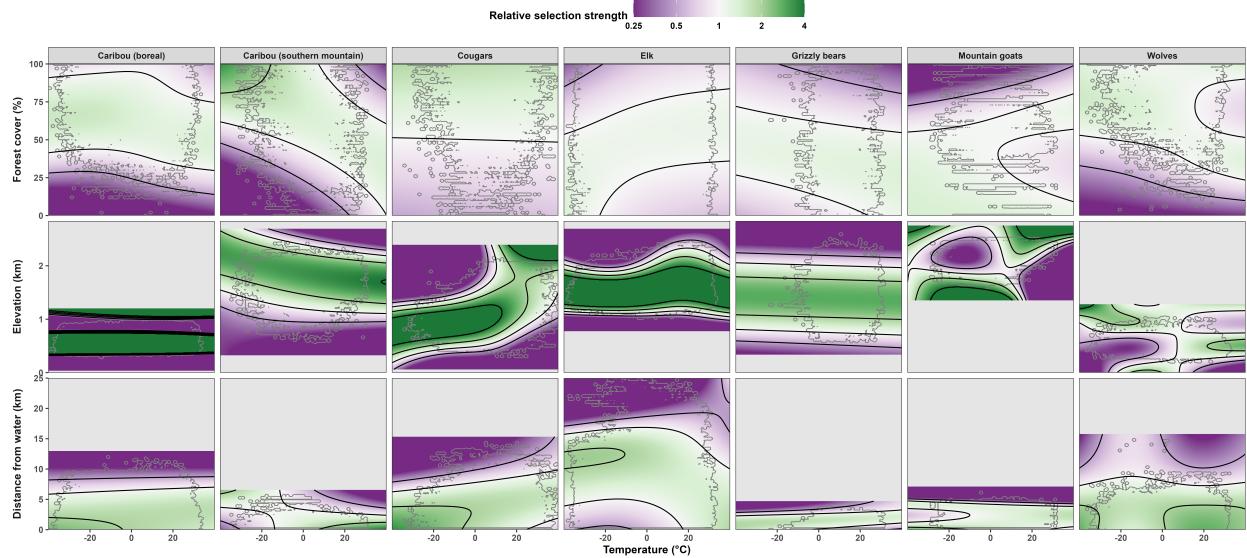


Figure 4: Mammals’ habitat selection depends on ambient temperature. Estimated relative selection strength (RSS) for forest cover (%), elevation (km), and distance from water (km) as a function of temperature. The grey contours indicate the extent of each species’ observed data. RSS values were re-centered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

339 3.3 Predicted changes in movement behaviour during the 21st century

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

353 Absolute relative changes in average yearly distance travelled were small under the best-

case SSP (0-4% change in 2100 relative to 2025). Under the worst-case SSP, absolute changes by 2100 (relative to 2025) ranged from ~2% (grizzly bears) to ~24% (cougars). Projected changes in 2100 varied spatially due to spatial heterogeneity in climate change projections (Fig. 6). Again, absolute changes were generally greatest under worse SSPs, but the direction of change at each location also varied across SSPs (most visible in cougars).

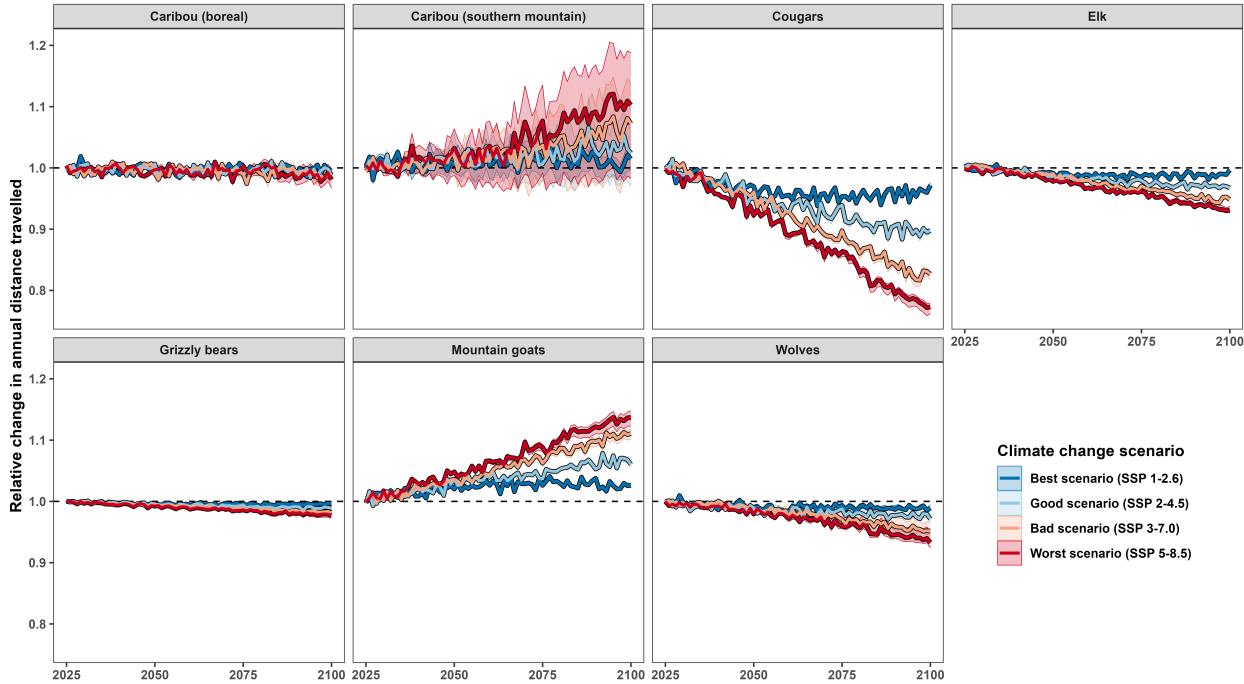


Figure 5: Species will alter their movement rates differently in response to climate change, but worse climate-change scenarios will result in the greatest change. Bold lines indicate the median change in distance travelled (probability of moving times speed when moving) due to predicted changes in temperature within each species' observed extent. Shaded areas indicate the 95th and 5th percentiles. Changes are relative to the mean predicted distance travelled at each location in 2025, averaged across the four Shared Socioeconomic Pathways (SSPs). Values > 1 indicate an increase, while values < 1 indicate a decrease. The projections only account for changes in movement frequency and speed, and they ignore changes in physiology or movement costs.

Median RSS was projected to decrease over time within the each species' observed range, but, again, changes were stronger under worse SSPs (Fig. 7). Decreases were most pronounced in areas with the lowest RSS and most severe for elk, mountain goats, pumas, and southern mountain caribou. Changes for boreal wolves and caribou were relatively negligible. Elk, cougars, and grizzly bears were predicted to increase their selection strength for top-RSS areas, and elk, mountain goats, cougars, and southern mountain caribou were predicted to further decrease their selection for areas with low RSS. Unsurprisingly, the

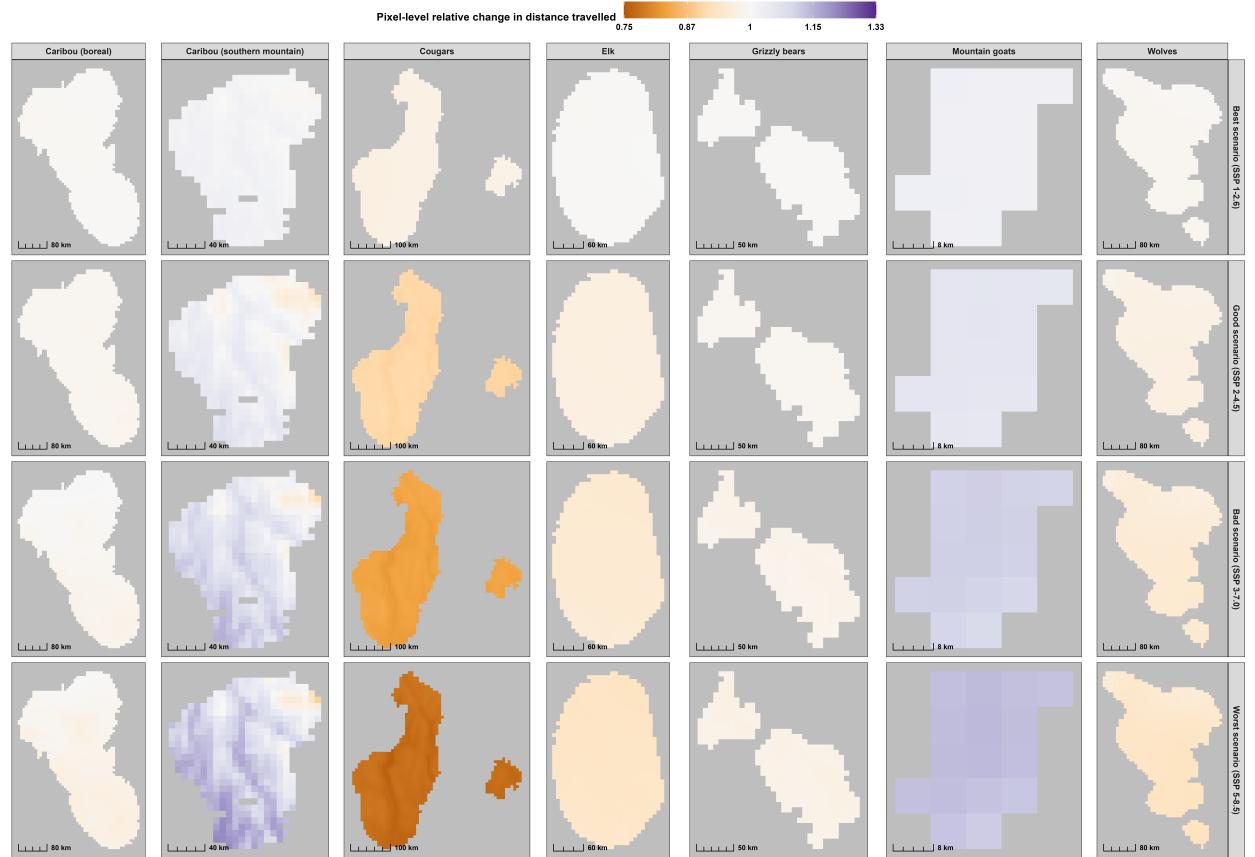


Figure 6: Climate change will impact each species' movement rates differently, but changes will also vary spatially. The color of each pixel indicates the predicted changes in distance traveled in 2100 at that pixel, relative to the value in 2025, averaged across all four scenarios. Values < 1 indicate a decrease, and values > 1 indicate an increase. For ease of readability, the color bar is on the \log_2 scale to help visualize patterns in doubling). The predictions only account for the predicted temperature throughout the areas and ignore environmental factors such as terrain slope, soil type, and forest density. All maps extend to each species' observed extent (Fig. 1) and are shown in the BC Albers Equal Area Conic projection (EPSG:3005).

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

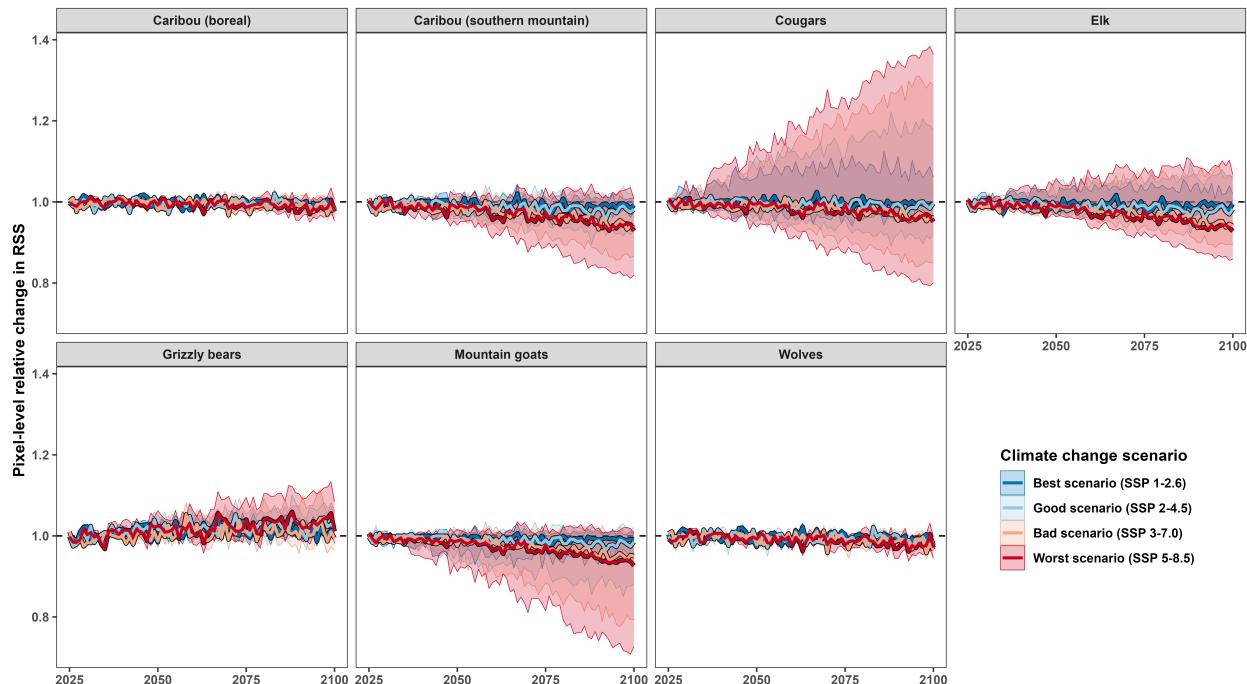


Figure 7: Species will alter their habitat selection differently in response to climate change, but worse climate-change scenarios will result in the greatest change. Bold lines indicate the change in median RSS due to predicted changes in temperature within each species' observed extent. Shaded areas indicate the 95th and 5th percentiles in change in RSS. Values > 1 indicate an increase, while values < 1 indicate a decrease. Changes are relative to each location's mean RSS in 2025, averaged across the four Shared Socioeconomic Pathways (SSPs).

370 4 Discussion

371 We have demonstrated that temperature is an important driver of how and where large mam-
 372 mals move, and that mammals alter their seasonal and daily cycles in movement behaviour
 373 in response to changes in temperature. However, predicting mammals' responses to climate
 374 change remains a challenge, as habitats warm rapidly and mammals are exposed to increas-
 375 ingly novel and extreme conditions (Diffenbaugh & Field, 2013; Botero *et al.*, 2015; IPCC,
 376 2023). We leveraged the flexibility and interpretability of HGAMs to estimate mammals'



Figure 8: Climate change will impact each species' relative selection strength (RSS) differently. The color scale indicates the predicted changes in RSS in 2100, relative to each location's average RSS in 2025 across all four scenarios (i.e., not relative to other pixels). Values < 1 indicate a decrease and values > 1 indicate an increase. For ease of readability, the color bar is on the \log_2 scale to help visualize patterns in doubling, and values are capped to 0.8 and 1.25 ($\approx 2^{\pm 0.322}$; original data ranged 0.71 to 1.93). All maps extend to each species' observed extent (Fig. 1) and are shown in the BC Albers Equal Area Conic projection (EPSG:3005).

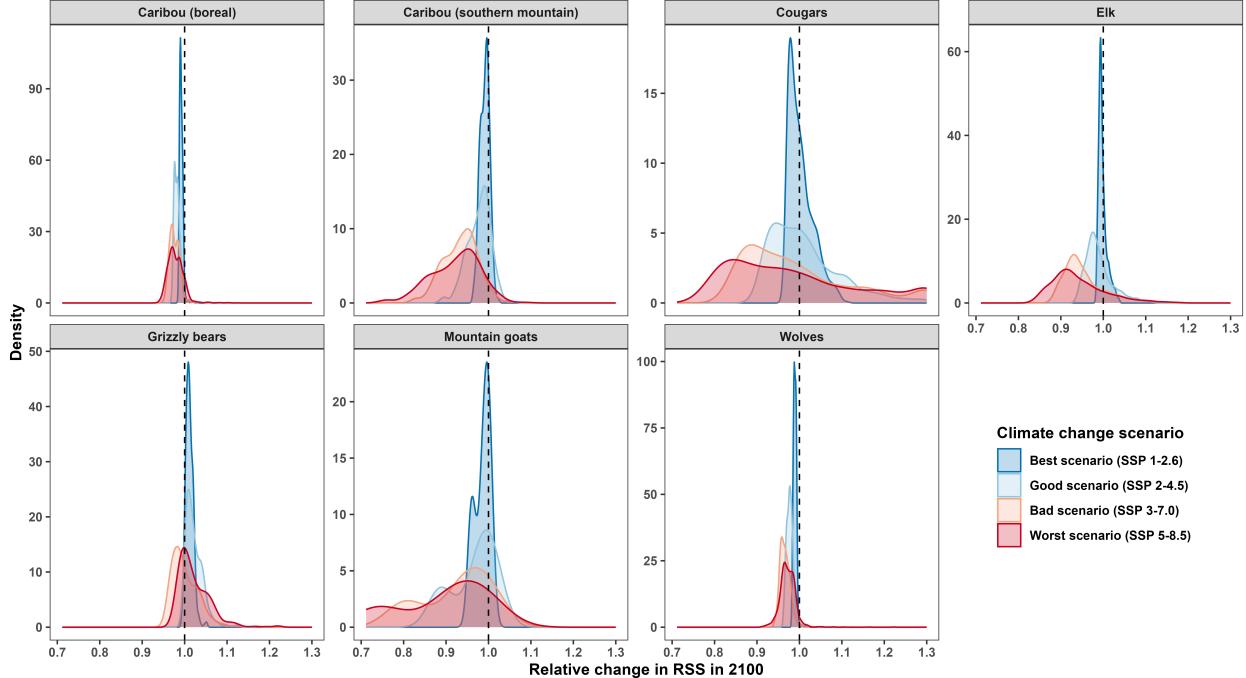


Figure 9: Climate change will cause species to decrease their selection strength for their current habitats, but worse climate change scenarios will have the greatest impact. The density plots indicate each species’ change in RSS in 2100 for their current habitat (Fig. 8), relative to each location’s RSS in 2025. Values < 1 indicate a decrease and values > 1 indicate an increase. For ease of readability, values > 1.3 were changed to 1.3 (original maximum: 1.93).

377 nonlinear responses to temperature without imposing rigid assumptions about the shape of
 378 the responses (Simpson, 2018, 2025). In particular, tensor product interaction terms were
 379 crucial for estimating smooth, nonlinear changes in daily and seasonal trends with tem-
 380 perature with data from multiple individuals. By allowing interaction terms to be smooth
 381 bivariate functions, we were able to quantify changes in movement behaviour without the
 382 need to discretize time into distinct windows (e.g., day/night and seasons). We were thus
 383 able to present results using relatively simple and interpretable surface plots (Figs. 3 and 4)
 384 that conveyed detailed and nuanced estimates of change. This framework was essential for
 385 estimating how mammals behave at extreme temperatures. Despite the recent increase in
 386 frequency of extreme weather events in western Canada (Bunnell *et al.*, 2011; Kienzle, 2018;
 387 Zhang *et al.*, 2023), such events remain relatively rare, so estimating mammals’ nonlinear re-
 388 sponses required the flexibility provided by GAMs (Wood, 2017). Additionally, hierarchical
 389 models allowed us to produce statistically sound estimates that accounted for differences in

390 behaviour and data availability across individuals (Pedersen *et al.*, 2019; Muff *et al.*, 2020;
391 McCabe *et al.*, 2021; Jeltsch *et al.*, 2025; Silva *et al.*, 2025). Still, GAMs' flexibility and
392 complexity can be a frustrating limitation if used too generously, so we suggest choosing
393 each smooth term's basis size (k) carefully. While penalized splines and REML can help
394 avoid unruly smooth terms, the penalty terms can struggle to restrict model complexity
395 when datasets are particularly large (Wood, 2017; Wood *et al.*, 2017).

396 Our results suggest that climate change will cause mammals to alter their seasonal move-
397 ment behaviour, but not all species will respond similarly. For example, hotter temperatures
398 caused boreal caribou to travel longer distances in fall, winter, and spring but less in sum-
399 mer, mirroring the findings of Stien *et al.* (2012), Leclerc *et al.* (2021), and Lessard *et*
400 *al.* (2025). The increase in movement rates during the colder seasons are likely partly due
401 to shallower snow depth that results in greater mobility (Pedersen *et al.*, 2021), but rising
402 temperatures during snowy seasons also increase the risk of rain-on-snow events, which limit
403 forage availability and increase time spent foraging (Stien *et al.*, 2012; Berger *et al.*, 2018;
404 Mezzini *et al.*, 2025). In contrast, the reduced movement rates during warmer summers
405 are likely mainly due to caribou's reduced movement rates and use of thermal refugia, given
406 ungulates' elevated risk of hyperthermia (Alston *et al.*, 2020; Verzuh *et al.*, 2023). Therefore,
407 although we predict that boreal caribou's yearly average movement rates will remain approx-
408 imately unchanged throughout the 21st century, the projections do not show the changes in
409 seasonal movement phenology. However, this is an important caveat, since the effects of
410 extreme temperatures are exacerbated by phenological mismatches with seasonal photope-
411 riod (Walker *et al.*, 2019), including the timing of molting and reproduction. Earlier growth
412 seasons in boreal and arctic regions have resulted in lower calf birth and survival (Post &
413 Forchhammer, 2008), while the lengthening of the growth season has allowed moose (*Alces*
414 *alces*) and deer to encroach on boreal caribou habitat and increase the density of coyotes
415 (*Canis latrans*), cougars, and wolves (Barber *et al.*, 2018; DeMars *et al.*, 2023), whose move-
416 ment behavior also depends on ambient temperature. Thus, rising temperatures affect more

417 than each individual species' movement behaviour; they have complex and interconnected
418 effects on an entire community and its trophic structure.

419 Work by Cunningham *et al.* (2021) discusses the importance of adopting a community-
420 level perspective when assessing the effects of climate change on animals' movement behavior
421 and phenology. For example, our results show that wolves responded to temperature by
422 altering their movement rates similarly to caribou. Consequently, as temperatures warm and
423 both species increase their movement rates in fall, winter, and spring, the resulting increase
424 in encounter rates (Martinez-Garcia *et al.*, 2020) will likely increase predation risk when
425 caribou are pregnant or with young calves. Additionally, while both species saw reduced
426 movement rates during hot summer days, boreal wolves' use of anthropogenic linear features
427 (e.g., roads, seismic lines) may allow them to reduce movement costs while increasing the
428 chances of encountering heat-stressed prey (Whittington *et al.*, 2011; Dickie *et al.*, 2017;
429 Dickie *et al.*, 2022). Furthermore, caribou that attempt to reduce predation risk from wolves
430 by avoiding wolf habitat may still risk increasing predation pressure from bears (Leblond *et*
431 *al.*, 2016) and other encroaching predators (DeMars *et al.*, 2023; Labadie *et al.*, 2023).

432 Considerations about changes in trophic interactions leads to another important caveat
433 about the results we present. The estimated changes movement behaviour cannot be fully
434 attributed to physiological responses to temperature alone, since other aspects of habitats'
435 seasonal phenology are (nonlinearly) correlated with temperature. For example, mountain
436 goats' lower movement rates at temperatures near 0°C in winter may be in part due to
437 increased movement difficulty, since melting snow and rain-on-snow events increase the en-
438 ergetic costs of movement (White, 2025) and encounter rates with predators (Sullender *et*
439 *al.*, 2023). However, milder temperatures can also increase plant growth, which allows goats
440 to spend more time foraging within and less time travelling across patches (Charnov, 1976;
441 White *et al.*, 2025). Therefore, figure 3 illustrates an estimate of the total effects of temper-
442 ature on each species movement rates, but it does not explicitly account for energetic costs.
443 Similarly, species' changes in habitat selection do not explicitly account for any changes

444 in physiological or energetic costs. Additionally, forest cover, elevation, and distance from
445 water are often correlated, so the estimated effects should be interpreted carefully, and they
446 may not be applicable outside our study areas. For example, both mountain goats and
447 elk selected for higher elevation as temperatures warmed, but our models did not explicitly
448 account for differences in forage availability at different altitudes.

449 Forage quality and availability is often a limiting factor for mammals' ability to adapt to
450 warming temperatures by moving to higher altitudes, since plants are slower to arrive in and
451 establish in new habitats than mammals, and the advance of herbivores can further limit
452 plants' ability to establish (Speed *et al.*, 2012; Diffenbaugh & Field, 2013). Consequently,
453 mammals that move to higher elevations may be forced to spend more time foraging (Mezzini
454 *et al.*, 2025), which will increase their energetic expenditure as well as their chances of
455 encountering predators (including cougars and grizzly bears) or competitors (Kohl *et al.*,
456 2019; Martinez-Garcia *et al.*, 2020; Tórrez-Herrera *et al.*, 2020; Smith *et al.*, 2023). If local
457 peaks become unsuitable habitat, and moving to nearby higher peaks requires traveling across
458 low-quality and high-risk habitat (Figure 8), habitat fragmentation may prevent movement
459 across ranges (White *et al.*, 2025). Translocating animals to locations with higher peaks may
460 help avoid such a scenario, but the success of relocations is species-dependent, and attempts
461 are not always successful (Ranc *et al.*, 2022; White *et al.*, 2025).

462 Future work should develop models that account for covariates that are specific to the
463 study species and area, such as forest age and disturbance (DeMars *et al.*, 2023), terrain
464 ruggedness (White & Gregovich, 2017), anthropogenic linear features (Dickie *et al.*, 2017),
465 and growing human presence (Sih *et al.*, 2011; Rice, 2022) and risk of human-wildlife conflict
466 (Abrahms *et al.*, 2023; Weststrate *et al.*, 2024). In particular, forests in western Canada are
467 highly dynamic over time (Zhang *et al.*, 2015), and fires size and burn severity have increased
468 in western Canada in recent decades (Parisien *et al.*, 2023; Zurowski, 2023). Thus, while our
469 use of a static raster of forest cover allowed for simpler models and climate change projections,
470 future studies should account for mammals' responses to temporal forest dynamics, including

471 the impacts of fire (Parisien *et al.*, 2023; Zurowski, 2023), harvest (Lochhead *et al.*, 2022)
472 and other extractive industries (Dickie *et al.*, 2017, 2024), as well as the subsequent forest
473 regeneration. However, the inclusion of temporally dynamic variables will require that any
474 future projections of species' behavior depend on temporally dynamic estimates of how such
475 variables will change over time with changes in climate and anthropogenic activity.

476 Species' adaptability to change depends mainly on its exposure, sensitivity, and adapt-
477 ability to changes, and growing evidence suggests that all three factors will limit mammals'
478 ability to adapt to climate change (Ameca y Juárez *et al.*, 2012; Diffenbaugh & Field, 2013).
479 Exposure to warming temperatures is widespread throughout the western Canada (Bunnell
480 *et al.*, 2011; Kienzle, 2018; Eum *et al.*, 2023), and changes in temperature and seasonal
481 phenology may be too rapid for many species to respond to (Diffenbaugh & Field, 2013).
482 Species' adaptability is further challenged by the the difficulty in responding to many con-
483 current, multifarious, and interconnected changes (Diffenbaugh & Field, 2013; Polazzo *et*
484 *al.*, 2024). Landscapes may thus become unable to support species and population sizes
485 they supported historically, and species may begin selecting against historical ranges in the
486 future (Williams & Blois, 2018). Therefore, it is crucial for conservationists to distinguish
487 between a species' ideal environmental space and its best available geographic space (*sensu*
488 Matthiopoulos, 2022). Accelerating multifarious change in species' movement behaviour and
489 energetic costs require conservation measures to be proactive and anticipate future changes,
490 especially when future conditions are projected to be substantially different from histori-
491 cal conditions. Polazzo *et al.* (2024) present a framework for estimating species' responses
492 to multifarious change using GAMs that is particularly useful when estimating species' re-
493 sponds to interactions between environmental variables (e.g., responses to changes in both
494 temperature and limiting nutrients). By accounting for the effects of multiple variables at
495 once, they demonstrate how a species' response to one variable can depend on other concur-
496 rent changes. Estimating responses to multifarious change is crucial in assessing the effects
497 of the effects of rising temperatures on community dynamics, including species' selection for

498 current habitats as well as changes in the habitats' carrying capacities and trophic interac-
499 tions. Protected areas must thus adapt to support populations not only in present conditions
500 but also as species' needs and behavior change over the coming decades (Simmons *et al.*,
501 2021; Livingstone *et al.*, 2023). Recent evidence has questioned whether current protected
502 areas will be effective in the long term (Loarie *et al.*, 2009; Diffenbaugh & Field, 2013;
503 Williams & Blois, 2018), and increasingly more experts have been calling for proactive and
504 long-term conservation. By identifying and actively protecting climate change refugia and
505 corridors, we may be able to reduce the effects of climate change on mammalian movement
506 behaviour and community-level responses and ensure that protected areas may be viable for
507 decades to come (Michalak *et al.*, 2018; Graham *et al.*, 2019; Stralberg *et al.*, 2020; Hua *et*
508 *al.*, 2022).

509 **Author contributions**

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

515 **References**

- 516 Aarts G, MacKenzie M, McConnell B, Fedak M, Matthiopoulos J (2008) [Estimating space-](#)
517 [use and habitat preference from wildlife telemetry data](#). *Ecography*, **31**, 140–160.
- 518 Abrahms B, Carter NH, Clark-Wolf TJ et al. (2023) [Climate change as a global amplifier of](#)
519 [human–wildlife conflict](#). *Nature Climate Change*, **13**, 224–234.
- 520 Alston JM, Joyce MJ, Merkle JA, Moen RA (2020) [Temperature shapes movement and](#)
521 [habitat selection by a heat-sensitive ungulate](#). *Landscape Ecology*, **35**, 1961–1973.
- 522 Alston JM, Fleming CH, Kays R et al. (2022) [Mitigating pseudoreplication and bias in](#)
523 [resource selection functions with autocorrelation-informed weighting](#). *Methods in Ecology*
524 [and Evolution](#), 2041–210X.14025.
- 525 Ameca y Juárez EI, Mace GM, Cowlishaw G, Pettorelli N (2012) [Natural population die-offs:](#)
526 [Causes and consequences for terrestrial mammals](#). *Trends in Ecology & Evolution*, **27**,
527 272–277.
- 528 Arechavala-Lopez P, Minguito-Frutos M, Follana-Berná G, Palmer M (2019) [Common octo-](#)
529 [pus settled in human-altered mediterranean coastal waters: From individual home range](#)
530 [to population dynamics](#) (ed Durif C). *ICES Journal of Marine Science*, **76**, 585–597.
- 531 Attias N, Oliveira-Santos LGR, Fagan WF, Mourão G (2018) [Effects of air temperature on](#)
532 [habitat selection and activity patterns of two tropical imperfect homeotherms](#). *Animal*
533 [Behaviour](#), **140**, 129–140.
- 534 Baddeley A, Rubak E, Turner R (2015) [Spatial point patterns: Methodology and applications](#)
535 [with r](#), 0th edn. Chapman; Hall/CRC.
- 536 Barber QE, Parisien M, Whitman E et al. (2018) [Potential impacts of climate change on](#)
537 [the habitat of boreal woodland caribou](#). *Ecosphere*, **9**, e02472.
- 538 Bartashevich P, Herbert-Read JE, Hansen MJ, Dhellemmes F, Domenici P, Krause J, Ro-
539 [manczuk P \(2024\) Collective anti-predator escape manoeuvres through optimal attack](#)
540 [and avoidance strategies](#). *Communications Biology*, **7**, 1586.

- 541 Basu A, Culpepper J, Blagrave K, Sharma S (2024) Phenological shifts in lake ice cover
542 across the northern hemisphere: A glimpse into the past, present, and the future of lake
543 ice phenology. *Water Resources Research*, **60**, e2023WR036392.
- 544 BC OGRIS (2018) Boreal caribou and wolf telemetry data.
- 545 Berger J, Hartway C, Gruzdev A, Johnson M (2018) Climate degradation and extreme icing
546 events constrain life in cold-adapted mammals. *Scientific Reports*, **8**, 1156.
- 547 Botero CA, Weissing FJ, Wright J, Rubenstein DR (2015) Evolutionary tipping points in
548 the capacity to adapt to environmental change. *Proceedings of the National Academy of
549 Sciences*, **112**, 184–189.
- 550 Brivio F, Apollonio M, Anderwald P, Filli F, Bassano B, Bertolucci C, Grignolio S (2024)
551 Seeking temporal refugia to heat stress: Increasing nocturnal activity despite predation
552 risk. *Proceedings of the Royal Society B: Biological Sciences*, **291**, 20231587.
- 553 Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory
554 of ecology. *Ecology*, **85**, 1771–1789.
- 555 Buderman FE, Hooten MB, Alldredge MW, Hanks EM, Ivan JS (2018) Time-varying preda-
556 tory behavior is primary predictor of fine-scale movement of wildland-urban cougars.
557 *Movement Ecology*, **6**, 22.
- 558 Bunnell FL, Kremsater LL, Wells RW (2011) Global weirding in british columbia: Climate
559 change and the habitat of terrestrial vertebrates. *Journal of Ecosystems and Manage-
560 ment*, **12**.
- 561 Burnett M (2023) climatenaR: Tools to access ClimateNA data.
- 562 Calabrese JM, Fleming CH, Gurarie E (2016) Ctmr: An r package for analyzing animal
563 relocation data as a continuous-time stochastic process (ed Freckleton R). *Methods in
564 Ecology and Evolution*, **7**, 1124–1132.
- 565 Carbeck K, Wang T, Reid JM, Arcese P (2022) Adaptation to climate change through
566 seasonal migration revealed by climatic versus demographic niche models. *Global Change
567 Biology*, **28**, 4260–4275.

- 568 Charnov EL (1976) Optimal foraging, the marginal value theorem. *Theoretical Population
569 Biology*, **9**, 129–136.
- 570 Ciuti S, Muhly TB, Paton DG, McDevitt AD, Musiani M, Boyce MS (2012) Human selection
571 of elk behavioural traits in a landscape of fear. *Proceedings of the Royal Society B:
572 Biological Sciences*, **279**, 4407–4416.
- 573 Cunningham SJ, Gardner JL, Martin RO (2021) Opportunity costs and the response of
574 birds and mammals to climate warming. *Frontiers in Ecology and the Environment*, **19**,
575 300–307.
- 576 Darlington S, Gooliaff T, Stent P, Hodges K, Ford AT (2025) Southern BC cougar project.
577 Movebank study 1620039803.
- 578 Deb JC, Forbes G, MacLean DA (2020) Modelling the spatial distribution of selected north
579 american woodland mammals under future climate scenarios. *Mammal Review*, **50**, 440–
580 452.
- 581 DeMars CA, Johnson CJ, Dickie M et al. (2023) Incorporating mechanism into conservation
582 actions in an age of multiple and emerging threats: The case of boreal caribou. *Ecosphere*,
583 **14**, e4627.
- 584 DeNicola VL, Mezzini S, Cagnacci F, Fleming CH (2025) Are your data too coarse for speed
585 estimation? Diffusion rates as an alternative measure of animal movement.
- 586 Dickie M, Serrouya R, McNay RS, Boutin S (2017) Faster and farther: Wolf movement on
587 linear features and implications for hunting behaviour (ed Du Toit J). *Journal of Applied
588 Ecology*, **54**, 253–263.
- 589 Dickie M, Serrouya R, Avgar T et al. (2022) Resource exploitation efficiency collapses the
590 home range of an apex predator. *Ecology*.
- 591 Dickie M, Serrouya R, Becker M et al. (2024) Habitat alteration or climate: What drives
592 the densities of an invading ungulate? *Global Change Biology*, **30**, e17286.
- 593 Dierauer JR, Allen DM, Whitfield PH (2021) Climate change impacts on snow and stream-
594 flow drought regimes in four ecoregions of british columbia. *Canadian Water Resources*

- 595 *Journal / Revue canadienne des ressources hydriques*, **46**, 168–193.
- 596 Diffenbaugh NS, Field CB (2013) **Changes in ecologically critical terrestrial climate condi-**
597 *tions*. *Science*, **341**, 486–492.
- 598 Duncan C, Chauvenet ALM, McRae LM, Pettorelli N (2012) **Predicting the future impact**
599 **of droughts on ungulate populations in arid and semi-arid environments** (ed Seebacher
600 F). *PLoS ONE*, **7**, e51490.
- 601 Dyer A, Brose U, Berti E, Rosenbaum B, Hirt MR (2023) **The travel speeds of large animals**
602 **are limited by their heat-dissipation capacities** (ed Hedenström A). *PLOS Biology*, **21**,
603 e3001820.
- 604 Elmore RD, Carroll JM, Tanner EP, Hovick TJ, Grisham BA, Fuhlendorf SD, Windels
605 SK (2017) **Implications of the thermal environment for terrestrial wildlife management**.
606 *Wildlife Society Bulletin*, **41**, 183–193.
- 607 Eum H-I, Fajard B, Tang T, Gupta A (2023) **Potential changes in climate indices in alberta**
608 **under projected global warming of 1.5–5 °c**. *Journal of Hydrology: Regional Studies*, **47**,
609 101390.
- 610 Fithian W, Hastie T (2013) **Finite-sample equivalence in statistical models for presence-only**
611 **data**. *The Annals of Applied Statistics*, **7**.
- 612 Fleming CH, Calabrese JM (2017) **A new kernel density estimator for accurate home-range**
613 **and species-range area estimation** (ed Dray S). *Methods in Ecology and Evolution*, **8**,
614 571–579.
- 615 Fleming CH, Calabrese JM (2023) **Ctmm: Continuous-time movement modeling**.
- 616 Fleming CH, Calabrese JM, Mueller T, Olson KA, Leimgruber P, Fagan WF (2014) **From**
617 **fine-scale foraging to home ranges: A semivariance approach to identifying movement**
618 **modes across spatiotemporal scales**. *The American Naturalist*, **183**, E154–E167.
- 619 Ford AT, Noonan MJ, Bollefer K, Gill R, Legebokow C, Serrouya R (2023) **The effects of**
620 **maternal penning on the movement ecology of mountain caribou**. *Animal Conservation*,
621 **26**, 72–85.

- 622 Fuller A, Mitchell D, Maloney SK, Hetem RS (2016) Towards a mechanistic understanding
623 of the responses of large terrestrial mammals to heat and aridity associated with climate
624 change. *Climate Change Responses*, **3**, 10.
- 625 Gerlich HS, Loboda S, Simpson GL, Savage J, Schmidt NM, Holmstrup M, Høye TT (2025)
626 Species' traits modulate rapid changes in flight time in high-arctic muscid flies under
627 climate change. *Proceedings of the Royal Society B: Biological Sciences*, **292**.
- 628 Giroux A, Ortega Z, Attias N, Desbiez ALJ, Valle D, Börger L, Rodrigues Oliveira-Santos
629 LG (2023) Activity modulation and selection for forests help giant anteaters to cope with
630 temperature changes. *Animal Behaviour*, **201**, 191–209.
- 631 Glass TW, Breed GA, Robards MD, Williams CT, Kielland K (2021) Trade-off between pre-
632 dation risk and behavioural thermoregulation drives resting behaviour in a cold-adapted
633 mesocarnivore. *Animal Behaviour*, **175**, 163–174.
- 634 Graham V, Baumgartner JB, Beaumont LJ, Esperón-Rodríguez M, Grech A (2019) Prioritiz-
635 ing the protection of climate refugia: Designing a climate-ready protected area network.
636 *Journal of Environmental Planning and Management*, **62**, 2588–2606.
- 637 Gulland FMD, Baker JD, Howe M et al. (2022) A review of climate change effects on marine
638 mammals in united states waters: Past predictions, observed impacts, current research
639 and conservation imperatives. *Climate Change Ecology*, **3**, 100054.
- 640 Hall LE, Chalfoun AD, Beever EA, Loosen AE (2016) Microrefuges and the occurrence of
641 thermal specialists: Implications for wildlife persistence amidst changing temperatures.
642 *Climate Change Responses*, **3**, 8.
- 643 Hannah L, Flint L, Syphard AD, Moritz MA, Buckley LB, McCullough IM (2014) Fine-
644 grain modeling of species' response to climate change: Holdouts, stepping-stones, and
645 microrefugia. *Trends in Ecology & Evolution*, **29**, 390–397.
- 646 Hegel TM, Mysterud A, Huettmann F, Stenseth NC (2010) Interacting effect of wolves and
647 climate on recruitment in a northern mountain caribou population. *Oikos*, **119**, 1453–
648 1461.

- 649 Hersbach H, Bell B, Berrisford P et al. (2023) ERA5 hourly data on single levels from 1940
650 to present.
- 651 Hetem RS, Fuller A, Maloney SK, Mitchell D (2014) Responses of large mammals to climate
652 change. *Temperature*, **1**, 115–127.
- 653 Hijmans RJ (2023) Terra: Spatial data analysis.
- 654 Hollister J, Shah T, Nowosad J, Robitaille AL, Beck MW, Johnson M (2023) Elevatr: Access
655 elevation data from various APIs.
- 656 Hou R, Chapman CA, Jay O, Guo S, Li B, Raubenheimer D (2020) Cold and hungry:
657 Combined effects of low temperature and resource scarcity on an edge-of-range temperate
658 primate, the golden snub-nose monkey. *Ecography*, **43**, 1672–1682.
- 659 Hua F, Bruijnzeel LA, Meli P et al. (2022) The biodiversity and ecosystem service contri-
660 butions and trade-offs of forest restoration approaches. *Science*, **376**, 839–844.
- 661 IPCC (2023) Climate change 2021 – the physical science basis: Working group i contribution
662 to the sixth assessment report of the intergovernmental panel on climate change, 1st edn.
663 Cambridge University Press.
- 664 Jahn M, Seebacher F (2022) Variations in cost of transport and their ecological consequences:
665 A review. *Journal of Experimental Biology*, **225**, jeb243646.
- 666 Jeltsch F, Roeleke M, Abdelfattah A et al. (2025) The need for an individual-based global
667 change ecology. *Individual-based Ecology*, **1**, 1–18.
- 668 Jessen C (2001) Temperature regulation in humans and other mammals. Springer Berlin
669 Heidelberg, Berlin, Heidelberg.
- 670 Johnson DH (1980) The comparison of usage and availability measurements for evaluating
671 resource preference. *Ecology*, **61**, 65–71.
- 672 Johnson HE, Lewis DL, Verzuh TL, Wallace CF, Much RM, Willmarth LK, Breck SW (2018)
673 Human development and climate affect hibernation in a large carnivore with implications
674 for human–carnivore conflicts (ed Bieber C). *Journal of Applied Ecology*, **55**, 663–672.
- 675 Kacelnik A, Krebs JR, Bernstein C (1992) The ideal free distribution and predator-prey

- 676 populations. *Trends in Ecology & Evolution*, **7**, 50–55.
- 677 Kays R, Davidson SC, Berger M et al. (2022) The movebank system for studying global
678 animal movement and demography. *Methods in Ecology and Evolution*, **13**, 419–431.
- 679 Kienzle SW (2018) Has it become warmer in alberta? Mapping temperature changes for the
680 period 1950–2010 across alberta, canada. *Canadian Geographies / Géographies canadi-
681 ennes*, **62**, 144–162.
- 682 Kohl MT, Ruth TK, Metz MC, Stahler DR, Smith DW, White PJ, MacNulty DR (2019) Do
683 prey select for vacant hunting domains to minimize a multi-predator threat? (ed Gaillard
684 J). *Ecology Letters*, **22**, 1724–1733.
- 685 Labadie G, Hardy C, Boulanger Y, Vanlandeghem V, Hebblewhite M, Fortin D (2023) Global
686 change risks a threatened species due to alteration of predator–prey dynamics. *Ecosphere*,
687 **14**, e4485.
- 688 Latham ADM, Latham MC, Mccutchen NA, Boutin S (2011) Invading white-tailed deer
689 change wolf–caribou dynamics in northeastern alberta. *The Journal of Wildlife Manage-
690 ment*, **75**, 204–212.
- 691 Leblond M, Dussault C, Ouellet J, St-Laurent M (2016) Caribou avoiding wolves face in-
692 creased predation by bears – caught between scylla and charybdis (ed Singh N). *Journal
693 of Applied Ecology*, **53**, 1078–1087.
- 694 Leclerc M, Leblond M, Le Corre M, Dussault C, Côté SD (2021) Determinants of migra-
695 tion trajectory and movement rate in a long-distance terrestrial mammal (ed Reyna R).
696 *Journal of Mammalogy*, **102**, 1342–1352.
- 697 Lessard É, Johnson CJ, St-Laurent M-H (2025) Local weather interacts with human distur-
698 bances to shape the behaviour of boreal caribou across a large climate gradient. *Biodi-
699 versity and Conservation*, **34**, 1115–1138.
- 700 Li Z, Wood SN (2020) Faster model matrix crossproducts for large generalized linear models
701 with discretized covariates. *Statistics and Computing*, **30**, 19–25.
- 702 Livingstone SW, Hughes J, Pither R, Fortin M-J (2023) Integrative adaptive management

- 703 to address interactions between biological invasions and protected area connectivity: A
704 canadian perspective (ed Smol JP). *FACETS*, **8**, 1–12.
- 705 Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD (2009) The velocity of
706 climate change. *Nature*, **462**, 1052–1055.
- 707 Lochhead KD, Kleynhans EJ, Muhly TB (2022) Linking woodland caribou abundance to
708 forestry disturbance in southern british columbia, canada. *The Journal of Wildlife Man-*
709 *agement*, **86**, e22149.
- 710 Mahony CR, Wang T, Hamann A, Cannon AJ (2022) A global climate model ensemble
711 for downscaled monthly climate normals over north america. *International Journal of*
712 *Climatology*, **42**, 5871–5891.
- 713 Martinez-Garcia R, Fleming CH, Seppelt R, Fagan WF, Calabrese JM (2020) How range res-
714 idency and long-range perception change encounter rates. *Journal of Theoretical Biology*,
715 **498**, 110267.
- 716 Matthiopoulos J (2022) Defining, estimating, and understanding the fundamental niches of
717 complex animals in heterogeneous environments. *Ecological Monographs*, **92**, e1545.
- 718 McCabe JD, Clare JD, Miller TA et al. (2021) Resource selection functions based on hierar-
719 chical generalized additive models provide new insights into individual animal variation
720 and species distributions. *Ecography*, **44**, 1756–1768.
- 721 McCain CM (2019) Assessing the risks to united states and canadian mammals caused
722 by climate change using a trait-mediated model (ed Heske E). *Journal of Mammalogy*,
723 gyz155.
- 724 McCain CM, King SRB (2014) Body size and activity times mediate mammalian responses
725 to climate change. *Global Change Biology*, **20**, 1760–1769.
- 726 McLellan ML, McLellan BN (2015) Effect of season and high ambient temperature on activity
727 levels and patterns of grizzly bears (*ursus arctos*) (ed Crocker DE). *PLOS ONE*, **10**,
728 e0117734.
- 729 McNab BK (1970) Body weight and the energetics of temperature regulation. *Journal of*

- 730 *Experimental Biology*, **53**, 329–348.
- 731 Melin M, Matala J, Mehtätalo L, Pusenius J, Packalen T (2023) **The effect of snow depth**
732 **on movement rates of GPS-collared moose.** *European Journal of Wildlife Research*, **69**,
733 21.
- 734 Merkle JA, Monteith KL, Aikens EO et al. (2016) **Large herbivores surf waves of green-up**
735 **during spring.** *Proceedings of the Royal Society B: Biological Sciences*, **283**, 20160456.
- 736 Mezzini S, Fleming CH, Medici EP, Noonan MJ (2025) **How resource abundance and resource**
737 **stochasticity affect organisms' range sizes.** *Movement Ecology*, **13**, 20.
- 738 Michalak JL, Lawler JJ, Roberts DR, Carroll C (2018) **Distribution and protection of climatic**
739 **refugia in north america.** *Conservation Biology*, **32**, 1414–1425.
- 740 Mota-Rojas D, Titto CG, Orihuela A et al. (2021) **Physiological and behavioral mechanisms**
741 **of thermoregulation in mammals.** *Animals*, **11**, 1733.
- 742 Muff S, Signer J, Fieberg J (2020) **Accounting for individual-specific variation in habi-**
743 **tat-selection studies: Efficient estimation of mixed-effects models using bayesian or fre-**
744 **quentist computation** (ed Wal EV). *Journal of Animal Ecology*, **89**, 80–92.
- 745 Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE (2008) **A**
746 **movement ecology paradigm for unifying organismal movement research.** *Proceedings of*
747 *the National Academy of Sciences*, **105**, 19052–19059.
- 748 Nathan R, Monk CT, Arlinghaus R et al. (2022) **Big-data approaches lead to an increased**
749 **understanding of the ecology of animal movement.** *Science*, **375**, eabg1780.
- 750 Newediuk L, Richardson ES, Biddlecombe BA et al. (2024) **Climate change, age acceleration,**
751 **and the erosion of fitness in polar bears.**
- 752 Noonan MJ, Fleming CH, Akre TS et al. (2019a) **Scale-insensitive estimation of speed and**
753 **distance traveled from animal tracking data.** *Movement Ecology*, **7**, 35.
- 754 Noonan MJ, Tucker MA, Fleming CH et al. (2019b) **A comprehensive analysis of autocor-**
755 **relation and bias in home range estimation.** *Ecological Monographs*, **89**, e01344.
- 756 Parisien M-A, Barber QE, Bourbonnais ML et al. (2023) **Abrupt, climate-induced increase in**

- 757 wildfires in british columbia since the mid-2000s. *Communications Earth & Environment*,
758 4, 309.
- 759 Pedersen EJ, Miller DL, Simpson GL, Ross N (2019) Hierarchical generalized additive models
760 in ecology: An introduction with mgcv. *PeerJ*, 7, e6876.
- 761 Pedersen SH, Bentzen TW, Reinking AK et al. (2021) Quantifying effects of snow depth on
762 caribou winter range selection and movement in arctic alaska. *Movement Ecology*, 9, 48.
- 763 Péron G, Fleming CH, De Paula RC, Mitchell N, Strohbach M, Leimgruber P, Calabrese JM
764 (2017) Periodic continuous-time movement models uncover behavioral changes of wild
765 canids along anthropization gradients. *Ecological Monographs*, 87, 442–456.
- 766 Peterson AN, Soto AP, McHenry MJ (2021) Pursuit and evasion strategies in the predator–
767 prey interactions of fishes. *Integrative and Comparative Biology*, 61, 668–680.
- 768 Pigeon KE, Stenhouse G, Côté SD (2016) Drivers of hibernation: Linking food and weather
769 to denning behaviour of grizzly bears. *Behavioral Ecology and Sociobiology*, 70, 1745–
770 1754.
- 771 Polazzo F, Limberger R, Pennekamp F, Ross SRP-J, Simpson GL, Petchey OL (2024) Mea-
772 suring the response diversity of ecological communities experiencing multifarious envi-
773 ronmental change. *Global Change Biology*, 30, e17594.
- 774 Post E, Forchhammer MC (2008) Climate change reduces reproductive success of an arctic
775 herbivore through trophic mismatch. *Philosophical Transactions of the Royal Society B:*
776 *Biological Sciences*, 363, 2367–2373.
- 777 Powers DR, Langland KM, Wethington SM, Powers SD, Graham CH, Tobalske BW (2017)
778 Hovering in the heat: Effects of environmental temperature on heat regulation in foraging
779 hummingbirds. *Royal Society Open Science*, 4, 171056.
- 780 R Core Team (2024) R: A language and environment for statistical computing. R Foundation
781 for Statistical Computing, Vienna, Austria.
- 782 Ranc N, Cagnacci F, Moorcroft PR (2022) Memory drives the formation of animal home
783 ranges: Evidence from a reintroduction (ed Coulson T). *Ecology Letters*, 25, 716–728.

- 784 Ratnayake HU, Kearney MR, Govekar P, Karoly D, Welbergen JA (2019) Forecasting wildlife
785 die-offs from extreme heat events. *Animal Conservation*, **22**, 386–395.
- 786 Riahi K, Vuuren DP van, Kriegler E et al. (2017) The shared socioeconomic pathways and
787 their energy, land use, and greenhouse gas emissions implications: An overview. *Global*
788 *Environmental Change*, **42**, 153–168.
- 789 Rice WL (2022) The conspicuous consumption of wilderness, or leisure lost in the wilderness.
790 *World Leisure Journal*, **64**, 451–468.
- 791 Rigby RA, Stasinopoulos DM (2005) Generalized additive models for location, scale and
792 shape (with discussion). *Journal of the Royal Statistical Society: Series C (Applied*
793 *Statistics)*, **54**, 507–554.
- 794 Sawyer H, Merkle JA, Middleton AD, Dwinnell SPH, Monteith KL (2019) Migratory plastic-
795 ity is not ubiquitous among large herbivores (ed Chapman J). *Journal of Animal Ecology*,
796 **88**, 450–460.
- 797 Schmidt NM, Grøndahl C, Evans AL et al. (2020) On the interplay between hypothermia
798 and reproduction in a high arctic ungulate. *Scientific Reports*, **10**, 1514.
- 799 Schwerdt L, De Villalobos AE, Ferretti N (2024) Ecological niche modelling and thermal pa-
800 rameters to assess the prevalence of an endemic tarantula: The endurance of grammostola
801 vachoni schiapelli & gerschman, 1961. *Journal of Insect Conservation*.
- 802 Sherwood SC, Huber M (2010) An adaptability limit to climate change due to heat stress.
803 *Proceedings of the National Academy of Sciences*, **107**, 9552–9555.
- 804 Sih A, Ferrari MCO, Harris DJ (2011) Evolution and behavioural responses to human-
805 induced rapid environmental change: Behaviour and evolution. *Evolutionary Applica-*
806 *tions*, **4**, 367–387.
- 807 Silva I, Fleming CH, Noonan MJ, Fagan WF, Calabrese JM (2025) Too few, too many, or
808 just right? Optimizing sample sizes for population-level inferences in animal tracking
809 projects.
- 810 Simmons BA, Nolte C, McGowan J (2021) Tough questions for the “30 × 30” conservation

- 811 agenda. *Frontiers in Ecology and the Environment*, **19**, 322–323.
- 812 Simpson GL (2018) Modelling palaeoecological time series using generalised additive models.
813 *Frontiers in Ecology and Evolution*, **6**, 149.
- 814 Simpson GL (2025) Method: Using generalized additive models in the animal sciences.
- 815 Slatyer RA, Umbers KDL, Arnold PA (2022) Ecological responses to variation in seasonal
816 snow cover. *Conservation Biology*, **36**, e13727.
- 817 Smith BJ, MacNulty DR, Stahler DR, Smith DW, Avgar T (2023) Density-dependent habitat
818 selection alters drivers of population distribution in northern yellowstone elk. *Ecology*
819 *Letters*, **26**, 245–256.
- 820 Sobie SR, Zwiers FW, Curry CL (2021) Climate model projections for canada: A comparison
821 of CMIP5 and CMIP6. *Atmosphere-Ocean*, **59**, 269–284.
- 822 Speed JDM, Austrheim G, Hester AJ, Mysterud A (2012) Elevational advance of alpine plant
823 communities is buffered by herbivory (ed Ejrnaes R). *Journal of Vegetation Science*, **23**,
824 617–625.
- 825 Stasinopoulos MD, Rigby RA (2007) Generalized additive models for location scale and
826 shape (GAMLSS) in r. *Journal of Statistical Software*, **23**.
- 827 Stien A, Ims RA, Albon SD et al. (2012) Congruent responses to weather variability in high
828 arctic herbivores. *Biology Letters*, **8**, 1002–1005.
- 829 Stralberg D, Carroll C, Nielsen SE (2020) Toward a climate-informed north american pro-
830 tected areas network: Incorporating climate-change refugia and corridors in conservation
831 planning. *Conservation Letters*, **13**, e12712.
- 832 Sullender BK, Cunningham CX, Lundquist JD, Prugh LR (2023) Defining the danger zone:
833 Critical snow properties for predator–prey interactions. *Oikos*, **2023**, e09925.
- 834 Tan M, Zhang S, Stevens M, Li D, Tan EJ (2024) Antipredator defences in motion: Animals
835 reduce predation risks by concealing or misleading motion signals. *Biological Reviews*,
836 **99**, 778–796.
- 837 Taylor CR, Heglund NC, Maloiy GMO (1982) Energetics and mechanics of terrestrial loco-

- 838 motion. I. Metabolic energy consumption as a function of speed and body size in birds
839 and mammals. *Journal of Experimental Biology*, **97**, 1–21.
- 840 Tórrez-Herrera LL, Davis GH, Crofoot MC (2020) Do monkeys avoid areas of home range
841 overlap because they are dangerous? A test of the risk hypothesis in white-faced capuchin
842 monkeys (*cebus capucinus*). *International Journal of Primatology*, **41**, 246–264.
- 843 Tuanmu M, Jetz W (2014) A global 1-km consensus land-cover product for biodiversity and
844 ecosystem modelling. *Global Ecology and Biogeography*, **23**, 1031–1045.
- 845 Turner NJ, Clifton H (2009) “It’s so different today”: Climate change and indigenous lifeways
846 in british columbia, canada. *Global Environmental Change*, **19**, 180–190.
- 847 Tysor CS (2025) Countergradient variation in lodgepole pine flowering phenology.
- 848 Verzuh TL, Rogers SA, Mathewson PD et al. (2023) Behavioural responses of a large,
849 heat-sensitive mammal to climatic variation at multiple spatial scales. *Journal of Animal
850 Ecology*, **92**, 619–634.
- 851 Walker WH, Meléndez-Fernández OH, Nelson RJ, Reiter RJ (2019) Global climate change
852 and invariable photoperiods: A mismatch that jeopardizes animal fitness. *Ecology and
853 Evolution*, **9**, 10044–10054.
- 854 Wang T, Hamann A, Spittlehouse D, Carroll C (2016) Locally downscaled and spatially
855 customizable climate data for historical and future periods for north america (ed Álvarez
856 I). *PLOS ONE*, **11**, e0156720.
- 857 Wells CP, Barbier R, Nelson S, Kanaziz R, Aubry LM (2022) Life history consequences of
858 climate change in hibernating mammals: A review. *Ecography*, **2022**, e06056.
- 859 Weststrate DK, Chhen A, Mezzini S, Safford K, Noonan MJ (2024) How climate change
860 and population growth will shape attendance and human-wildlife interactions at british
861 columbia parks. *Journal of Sustainable Tourism*, 1–15.
- 862 White KS (2025) Population ecology of mountain goats in relation to climate, weather and
863 snow avalanches. PhD thesis, University of Victoria.
- 864 White KS, Gregovich DP (2017) Mountain goat resource selection in relation to min-

- 865 ing-related disturbance. *Wildlife Biology*, **2017**, 1–12.
- 866 White KS, Cadsand B, Côté SD et al. (2025) Mountain sentinels in a changing world:
867 Review and conservation implications of weather and climate effects on mountain goats
868 (*Oreamnos americanus*). *Global Ecology and Conservation*, **57**, e03364.
- 869 Whittington J, Hebblewhite M, DeCesare NJ, Neufeld L, Bradley M, Wilmshurst J, Musiani
870 M (2011) Caribou encounters with wolves increase near roads and trails: A time-to-event
871 approach. *Journal of Applied Ecology*, **48**, 1535–1542.
- 872 Williams JE, Blois JL (2018) Range shifts in response to past and future climate change:
873 Can climate velocities and species' dispersal capabilities explain variation in mammalian
874 range shifts? *Journal of Biogeography*, **45**, 2175–2189.
- 875 Winter VA, Smith BJ, Berger DJ et al. (2024) Forecasting animal distribution through in-
876 dividual habitat selection: Insights for population inference and transferable predictions.
877 *Ecography*, e07225.
- 878 Wood SN (2017) Generalized additive models: An introduction with r, Second edition edn.
879 CRC Press/Taylor & Francis Group, Boca Raton.
- 880 Wood SN, Goude Y, Shaw S (2015) Generalized additive models for large data sets. *Journal*
881 *of the Royal Statistical Society: Series C (Applied Statistics)*, **64**, 139–155.
- 882 Wood SN, Li Z, Shaddick G, Augustin NH (2017) Generalized additive models for gigadata:
883 Modeling the u.k. Black smoke network daily data. *Journal of the American Statistical
884 Association*, **112**, 1199–1210.
- 885 Woo-Durand C, Matte J-M, Cuddihy G, McGourdji CL, Venter O, Grant JWA (2020) In-
886 creasing importance of climate change and other threats to at-risk species in canada.
887 *Environmental Reviews*, **28**, 449–456.
- 888 Xu W, Barker K, Shawler A et al. (2021) The plasticity of ungulate migration in a changing
889 world. *Ecology*, **102**, e03293.
- 890 Zhang J, Huang S, He F (2015) Half-century evidence from western canada shows forest
891 dynamics are primarily driven by competition followed by climate. *Proceedings of the*

- 892 *National Academy of Sciences*, **112**, 4009–4014.
- 893 Zhang X, Zhou T, Zhang W et al. (2023) Increased impact of heat domes on 2021-like heat
894 extremes in north america under global warming. *Nature Communications*, **14**, 1690.
- 895 Zurowski M (2023) The summer canada burned: The wildfire season that shocked the world.
- 896 Postmedia / Greystone Books, Vancouver, 183 p.