

The heat is on: Rising temperatures alter how and where mammals
move

Stefano Mezzini^{1,2} Chris H. Fleming^{3,4} Siobhan Darlington^{1,2}

Adam T. Ford^{1,2} TJ Gooliaff⁵ Karen E. Hodges^{1,2} 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.

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Abstract

Widespread warming during the last century has caused many terrestrial mammals to change how and where they move, with cascading effects on fitness, habitat selection, and community structure. Previous studies have estimated the effects of temperature on mammalian movement behaviour, but many did not disentangle them from seasonal behaviour cycles. Consequently, it is still unclear how mammals will adapt their movement behaviour in the 21st century. We address this gap by using continuous-time movement models and hierarchical generalized additive models to quantify the effects of temperature on the movement rates and habitat selection of six large-bodied mammalian species throughout western Canada between 1998 and 2023. We show that temperature is a strong determinant of how and where mammals move, and we predict that climate change will have significant impacts on mammals' movement rates and habitat selection throughout the 21st century. We found that species did not respond uniformly to rising temperatures, so community-level responses will likely be complex as some species move more and others less. Median habitat selection strength decreased for all species, but some species showed increased selection strength for higher altitudes. Consequently, our results suggest that all six species may shift their range in the coming decades as their selection strength for their current ranges weakens. As climate change exposes mammals to novel environmental conditions, predicting changes in animal behaviour and community structure will become crucial for effectively and proactively understanding mammalian movement behaviour and protecting high-quality habitat. We thus present our work using a flexible approach that can be adapted for different species and spatiotemporal scales, and we conclude by providing suggestions for future research, with particular attention to the study design, statistical modeling, and forecasting.

¹ **1 other refs**

- ² • Gerlich *et al.* (2025): effects of temperature on fly movement in the arctic
- ³ • “Potential changes in climate indices in Alberta under projected global warming of
- ⁴ 1.5–5 °C” (<https://www.sciencedirect.com/science/article/pii/S2214581823000770#fig0015>)
- ⁵ • Global vulnerability of marine mammals to global warming: <https://doi.org/10.1038/s41598-019-57280-3>
- ⁶ • marine turtles shift and lose habitat with temperature: <https://www.science.org/doi/10.1126/sciadv.adw4495>
- ⁷ • changes in temperature change phenology and movement behaviour as a consequence
- ⁸ Gerlich *et al.* (2025)
- ⁹ • Walker *et al.* (2019): Global climate change and invariable photoperiods: {A} mismatch that jeopardizes animal fitness
- ¹⁰
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¹⁴ **2 Introduction**

¹⁵ For most animals, movement is a rapid and low-cost response to a variety of stimuli (Nathan
¹⁶ *et al.*, 2008). Animals move to optimize resource use (e.g., food, water, shelter; Charnov,
¹⁷ 1976; Kacelnik *et al.*, 1992; Merkle *et al.*, 2016; Mezzini *et al.*, 2025), optimize habitat use
¹⁸ (Schwerdt *et al.*, 2024; Winter *et al.*, 2024), and avoid predators and competitors (Tórrez-
¹⁹ Herrera *et al.*, 2020; Peterson *et al.*, 2021; Bartashevich *et al.*, 2024; Tan *et al.*, 2024).
²⁰ However, ambient temperature affects mammals' movement rates by altering the energetic
²¹ cost of movement (McNab, 1970; Taylor *et al.*, 1982; Brown *et al.*, 2004; Fuller *et al.*, 2016;
²² Jahn & Seebacher, 2022) and the risk of hyperthermia (Hetem *et al.*, 2014; Dyer *et al.*, 2023).
²³ Animals may search for a short-term buffer from extreme heat or cold via thermal refugia
²⁴ (Hannah *et al.*, 2014; Elmore *et al.*, 2017; Attias *et al.*, 2018; Arechavala-Lopez *et al.*, 2019;
²⁵ Gulland *et al.*, 2022), which may even be preferred over forage abundance (Hall *et al.*, 2016).
²⁶ By altering mammals' movement speed and habitat use (jointly, their movement behaviour:
²⁷ Nathan *et al.*, 2008, 2022), ambient temperature also affects the consequences of movement
²⁸ behaviour (Alston *et al.*, 2020; Giroux *et al.*, 2023), such as encounter rates with resources
²⁹ (Mezzini *et al.*, 2025), humans (Weststrate *et al.*, 2024), predators, prey, or competitors
³⁰ (Martinez-Garcia *et al.*, 2020; Glass *et al.*, 2021; Brivio *et al.*, 2024). Behavioural changes
³¹ to temperature are exacerbated in extreme cold (Wilson *et al.*, 2001; Berger *et al.*, 2018)
³² and extreme heat (Powers *et al.*, 2017; Alston *et al.*, 2020; Giroux *et al.*, 2023; Verzuh *et al.*,
³³ 2023).

³⁴ Mammals are particularly susceptible to adverse effects from excessive heat (Sherwood &
³⁵ Huber, 2010). While extreme cold often leads to reduced movement, provided that individ-
³⁶ uals can find refuge and take advantage of their body heat (Berger *et al.*, 2018; Hou *et al.*,
³⁷ 2020; Glass *et al.*, 2021), extreme heat can often result in more severe physiological damage
³⁸ in a shorter span of time (Jessen, 2001; Sherwood & Huber, 2010; Mota-Rojas *et al.*, 2021;
³⁹ Newediuk *et al.*, 2024). Due to mammals' difficulty at dissipating heat, particularly when

40 ambient temperatures are near or above their body temperature, they are particularly sen-
41 sitive to extreme heat, especially with increasing body size (Dyer *et al.*, 2023; Verzuh *et al.*,
42 2023). Furthermore, species that experience narrow temperature ranges (i.e., ‘temperature
43 specialists’) tend to be more sensitive to changes (e.g., giant anteaters, *Myrmecophaga tri-*
44 *dactyla*: Giroux *et al.*, 2023), while species that experience wide ranges of temperature vari-
45 ation (i.e., ‘temperature generalists’) can adapt more easily to change (Levins, 1974; Botero
46 *et al.*, 2015; Dupont *et al.*, 2024). Still, generalists’ greater adaptability is tested when they
47 are subject to changes that are more severe (McCain, 2019; Rantanen *et al.*, 2022), affect
48 many factors at once (e.g., temperature, snow depth, ecosystem phenology, and resource
49 availability: Polazzo *et al.*, 2024), or are too rapid and severe to respond within a lifetime
50 or a few generations (Levins, 1974; Fuller *et al.*, 2016; Xu *et al.*, 2021).

51 In the last century, many ecosystems experienced widespread warming that resulted in
52 milder and shorter winters, hotter and longer summers, and a greater risk of extremely high
53 temperatures (IPCC, 2023). As heat stress intensifies over the next 100 years, mammals will
54 continue to suffer impacts on their fitness, movement rates, and habitat selection (Deb *et*
55 *al.*, 2020; Woo-Durand *et al.*, 2020), which will be exacerbated by more frequent and intense
56 extreme events (Bunnell *et al.*, 2011) and anthropogenic habitat loss, modification, and frag-
57 mentation (Sawyer *et al.*, 2009; Sih *et al.*, 2011; Weststrate *et al.*, 2024). It remains unclear
58 how or whether species will be able to respond to climate change in the current century (Deb
59 *et al.*, 2020; Woo-Durand *et al.*, 2020; Verzuh *et al.*, 2023), especially if populations fail to
60 adapt to changes (Botero *et al.*, 2015; Sawyer *et al.*, 2019) or are physiologically incapable
61 to do so (Sherwood & Huber, 2010; Williams & Blois, 2018). Preparing for and responding
62 to future changes require a comprehensive understanding of how temperature will affect how
63 and where mammals move, as well as the implications such changes will have on species’
64 adaptability and overall community structure. Recent work has documented the effects of
65 climate change on mammals’ ranges (Leclerc *et al.*, 2021), movement behaviour (Melin *et al.*,
66 2023), thermoregulation (Mota-Rojas *et al.*, 2021), and trait-based responses (e.g., body size,

67 activity time, and elevational and latitudinal distribution McCain, 2019). However, there
68 remains a need for fine-scale estimates of the effects of temperature on mammals' movement
69 behaviour and quantitative predictions of how their behaviour will respond to climate change
70 in the current century (IPCC, 2023).

71 Western Canada is currently experiencing rapid widespread warming (Turner & Clifton,
72 2009; Kienzle, 2018; Dierauer *et al.*, 2021), phenological shifts (Kienzle, 2018; Basu *et al.*,
73 2024; Tysor, 2025), and more frequent and intense extreme events (Zhang *et al.*, 2023),
74 including forest fires (Zurowski, 2023). As we approach the deadline for the Kunming-
75 Montreal Global Biodiversity Framework (i.e., the “30 by 30” initiative), a global effort to
76 conserve 30% of the world’s lands and oceans by 2030 (Convention on Biological Diversity,
77 2022), Canadian decision makers must understand which areas will be of greatest value for
78 maximizing and protecting biodiversity not only for current conditions but future decades,
79 too. Failing to understand how climate change will affect mammalian movement behaviour
80 will hinder our ability to respond to the current climate crisis and make decisions that are
81 viable in the long term. Furthermore, understanding how temperature affects individual
82 species is the first step towards understanding how temperature impacts the community
83 dynamics (Hegel *et al.*, 2010) and habitat phenology (Bunnell *et al.*, 2011; Duncan *et al.*,
84 2012; Merkle *et al.*, 2016; Slatyer *et al.*, 2022).

85 In this paper, we quantify the effects of proximal air temperature on mammalian move-
86 ment behaviour, namely movement rates and habitat selection of six large-bodied terrestrial
87 mammal species in western Canada (wolves: *Canis lupus*, elk: *Cervus canadensis*, moun-
88 tain goats: *Oreamnos americanus*, cougars: *Puma concolor*, boreal and southern mountain
89 caribou: *Rangifer tarandus*, and grizzly bears: *Ursus arctos horribilis*; Table 1). Using over
90 25 years of telemetry data throughout a large spatial range of western Canada and hourly
91 air temperature data, we estimate how these mammals altered their probability of move-
92 ment, speed when moving, and habitat selection in response to temperature. We then pair
93 the estimated responses with climate change projections to forecast the species’ movement

94 behaviour during the 21st century under different climate-change scenarios (referred to as
 95 Shared Socioeconomic Pathways, SSP, Riahi *et al.*, 2017). We discuss the consequences of
 96 these changes in movement behaviour at the individual, population, and community levels.
 97 We also provide directions for future research and solutions for overcoming some common
 98 data limitations.

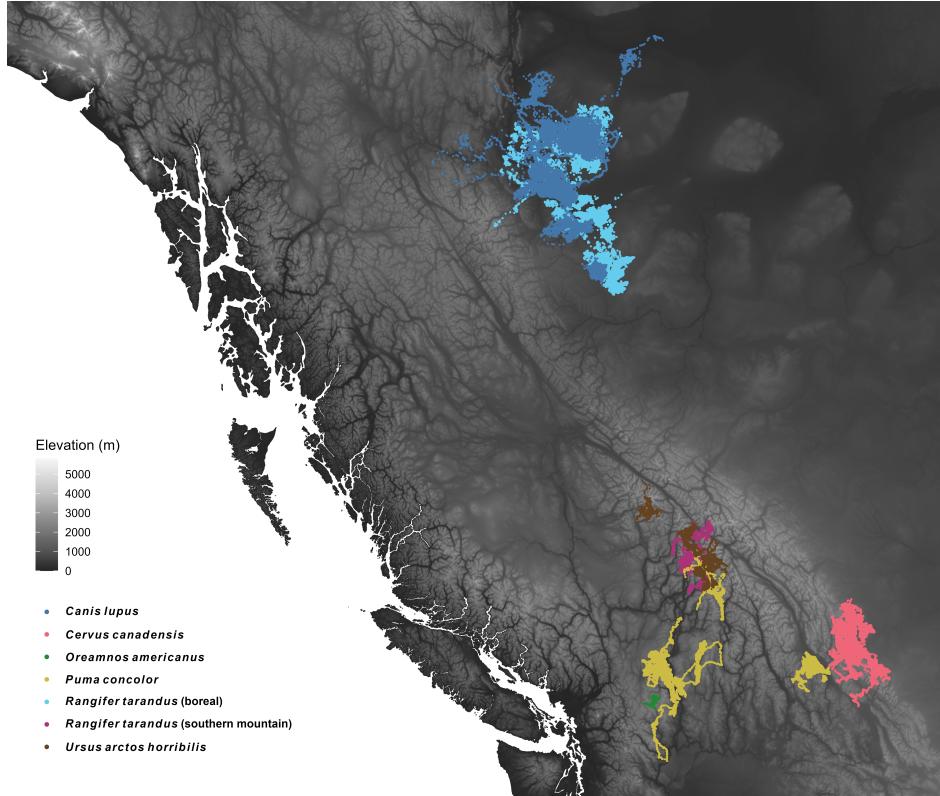


Figure 1: GPS telemetry data for the six species in this study (dots) over a digital elevation model for the study area.

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

Species	Start	End	Δt (hours)	Animals	Has speed
<i>Canis lupus</i>	2013-01-27	2017-08-29	0.25	39	39
<i>Cervus canadensis</i>	2007-01-13	2013-11-20	2.00	169	169
<i>Oreamnos americanus</i>	2019-06-25	2023-10-05	6.25	11	10
<i>Puma concolor</i>	2006-02-05	2021-07-13	2.00	29	29
<i>Rangifer tarandus</i> (boreal)	2011-03-02	2018-01-04	13.00	146	131
<i>Rangifer tarandus</i> (s. mountain)	1998-03-21	2009-06-07	6.00	22	20

Species	Start	End	Δt (hours)	Animals	Has speed
<i>Ursus arctos horribilis</i>	2004-09-30	2009-09-07	1.00	18	18

99 3 Methods

100 3.1 Datasets used

101 This study leverages four main datasets: (1) a multi-species collection of GPS telemetry
 102 data (Fig. 1); (2) historical hourly air temperature from the ERA5 reanalyzed dataset (Euro-
 103 pean Center for Medium-range Weather Forecasting; Hersbach *et al.*, 2023); (3) temporally
 104 static rasters of percent forest cover, elevation, and distance from water; and (4) climate
 105 change projections under four Shared Socioeconomic Pathways (SSPs; Riahi *et al.*, 2017).

106 While we acknowledge there are other important variables (e.g., forest type, structure, and
 107 age; terrain slope and aspect), we limited our models to only use three simple variables
 108 for the sake of parsimony and comparability across species. See the discussion section for
 109 additional detail on the advantages and limitations of using such simple models.

110 3.1.1 GPS telemetry data

111 Elk (*Cervus canadensis*) data from Ciuti *et al.* (2012) were downloaded from Movebank
 112 (study name: Elk in southwestern Alberta, see Kays *et al.*, 2022). Boreal caribou (*Rangifer*
 113 *tarandus*) and wolf (*Canis lupus*) telemtries were acquired from a data repository of the
 114 British Columbia Oil and Gas Research and Innovation Society (BC OGRIS) that was col-
 115 lected as part of the boreal caribou radio-collaring program of the BC OGRIS Research
 116 and Effectiveness Monitoring Board (REMB; BC OGRIS, 2018). **MISSING INFO ON**
 117 **OTHER TELEMETRY DATA.** From the full set of telemetry data, we removed a total
 118 of 2396 problematic GPS locations (0.16%, including collar calibration data) after inspect-
 119 ing diagnostic plots of (1) distance from the median location, (2) straight-line displacement
 120 between locations, (3) turning angle, and (4) time interval between consecutive points. Par-

121 ticular attention was paid to points with large turning angles ($\gtrsim 170^\circ$) and excessively high
122 straight-line displacement, especially if antecedent and subsequent points indicated relatively
123 stationary behaviour (Appendix A).

124 3.1.2 Historical temperature data and climate change projections

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

131 We used the the `climatenetR` package (v. 1.0, Burnett, 2023) for `R` and `ClimateNA` (v.
132 7.4.2; Wang *et al.*, 2016; Mahony *et al.*, 2022) to obtain projected average monthly temper-
133 atures from 2020 to 2100 at a 0.08° spatial resolution. Since the climate projections only
134 provided monthly means and ranges but no measures of variance or distributional assump-
135 tions, we used the historical data for western Canada from 1998 to 2023 (extremes included)
136 to estimate the monthly variation in temperature, which we defined as σ_T^2 , the variance at
137 location $\langle x, y \rangle$ in month m for each year (e.g., the variance at coordinates $\langle -119.40, 49.94 \rangle$
138 in April 2005). We then modeled the estimated variance using a Generalized Additive Model
139 for Location and Scale (GAMLS, Rigby & Stasinopoulos, 2005; Stasinopoulos & Rigby, 2007;
140 section 7.9 in Wood, 2017) using the `mgcv` package for `R` (v. 1.9-1, Wood, 2017). The linear
141 predictor for the location (i.e., the mean) included smooth terms of: each year's estimated
142 within-pixel monthly mean temperature ($\hat{\mu}_T$), month (m), a two-dimensional smooth of spa-
143 tial coordinates $\langle x, y \rangle$, and a tensor product interaction term of month and space to allow
144 for seasonal terms to vary smoothly over space. The linear predictor for the scale term,
145 which governs the mean-variance relationship (table 3.1 on p. 104 of Wood, 2017), included
146 smooth terms of the monthly mean temperature, month, and space. We did not include

¹⁴⁷ smooth terms of year to avoid unrealistic projections when extrapolating beyond 2023.

¹⁴⁸ The model was thus

$$\begin{cases} \sigma_T^2 \sim \text{Gamma}(\mu_{\sigma_T^2}, \nu_{\sigma_T^2}) \\ \mathbb{E}(\sigma_T^2) = \mu_{\sigma_T^2} \\ \mathbb{V}(\sigma_T^2) = (\mu_{\sigma_T^2})^2 / \nu_{\sigma_T^2} \\ \log(\mu_{\sigma^2}) = \beta_{L,0} + f_{L,1}(\mu_T) + f_{L,2}(m) + f_{L,3}(x, y) + f_{L,4}(x, y, m) \\ \log(\nu_{\sigma^2}) = \beta_{S,0} + f_{S,1}(\mu_T) + f_{S,2}(m) + f_{S,3}(x, y) \end{cases}, \quad (1)$$

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 **3.1.3 Resource rasters**

165 We estimated percent forest cover and distance from water using the rasters created by
166 Tuanmu & Jetz (2014). We calculated total forest cover by summing the temporally
167 static rasters of evergreen/deciduous needle-leaf trees, evergreen broadleaf trees, deciduous
168 broadleaf trees, and mixed/other trees (raster classes 1-4, respectively). We converted the
169 raster of percent cover of open water (class 12) to a binary raster of pixels with water
170 (cover > 0%) or without water (cover = 0%) and then calculated each pixel's distance
171 from the nearest pixel with water using the `distance()` function from the `terra` package.
172 Finally, we obtained two digital elevation models using the `get_elev_raster()` function
173 from the `elevatr` package (v. 0.99.0, Hollister *et al.*, 2023). We used a raster with a zoom
174 of 6 (a resolution of 0.009°) for model fitting and one with a zoom of 3 (a resolution of
175 0.08°) for downloading climate change projections via `climatenar`. All final rasters and
176 code are available in the GitHub repository associated with this manuscript (see the Data
177 Availability Statement).

178 **3.2 Estimating mammals' instantaneous speeds**

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

186 Since `ctmm`'s movement models assume a single moving state with stochastic but non-
187 zero speed, we corrected data-informed speeds so that the minimum instantaneous speed
188 could be 0. We performed this correction by subtracting each model's mean speed while
189 assuming speeds were χ^2 -distributed. The function we used is available on GitHub (see the

190 Data Availability Statement). To avoid artifacts due to excessively small, non-zero speeds,
191 we determined whether an animal was moving or not using a k -means algorithm with 2
192 clusters for each species' distribution of detrended speeds. When the algorithm clearly failed
193 to discriminate between states, we estimated the split point using the inflection points in
194 histograms of the detrended speeds (Fig. B1).

195 **3.3 Estimating the effects of temperature on mammals' movement behaviour**

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

207 The two following sections detail the statistical framework and models we used to estimate
208 the effect on temperature on the six species' movement behavior. To assess the importance of
209 including temperature as an explicit covariate (as opposed to including its effects with time
210 of day and day of year), we fit models with and without smooth effects of temperature and
211 compared the fits of the two sets of models via analyses of deviance (a form of generalized
212 likelihood ratio tests) following the methods of Section 3.3 in Wood (2017). See Appendix
213 B for additional information.

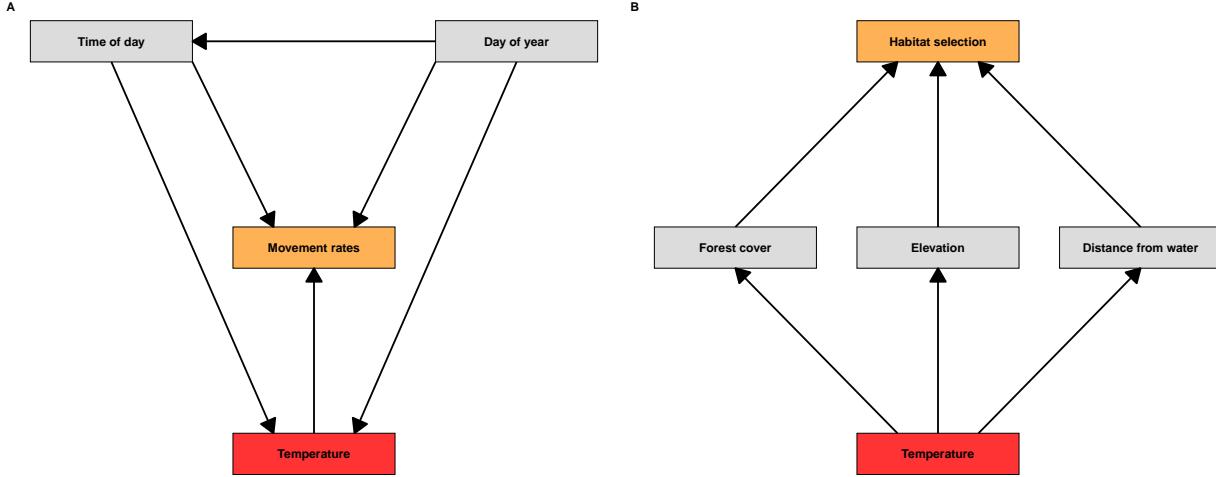


Figure 2: Directed Acyclical Graphs (DAGs) assumed for inferring the causal effects of temperature on each species' movement behaviour. (A) Ambient temperature affects mammals' movement rates (i.e. probability of moving, speed when moving, and distance traveled), but temperature is influenced by time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

214 3.3.1 Effects of temperature on movement rates

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

226 The HGAMs (equations (2) and (3)) included fixed-effect intercepts for each species
 227 (β_s), random intercepts for each animal (Z_a), and species-level `by` smooths that allowed
 228 independent smoothness parameters for each species (model I in Figure 4 of Pedersen *et*

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

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

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

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

²⁴⁶ In both models, β_s indicates a fixed intercept for species s , Z_a indicates a Gaussian random
²⁴⁷ effect for animal a (of species s), $f_{j,s}$ indicates the j^{th} smooth function for species s , and
²⁴⁸ functions with two variables indicate tensor product interaction terms. The model code used
²⁴⁹ to fit the models is available in Appendix B.

²⁵⁰ **3.3.2 Effects of temperature on habitat selection**

²⁵¹ We estimated the effects of temperature on each species' selection for percent forest cover
²⁵² (`forest_perc`), elevation (`elevation_m`), and distance from water (`dist_water_m`) by fit-
²⁵³ ting a Hierarchical Resource Selection Function (HRSF) for each species. We fit each HRSF
²⁵⁴ using an HGAM with a Poisson family of distributions and log link function (Appendix B;
²⁵⁵ Aarts *et al.*, 2008). After removing non-resident individuals (Table B1), we accounted for the
²⁵⁶ spatiotemporal autocorrelation in the telemetry locations by weighting each point based on
²⁵⁷ the telemetry's Autocorrelated Kernel Density Estimate (Fleming & Calabrese, 2017; Noo-
²⁵⁸ nan *et al.*, 2019b; Alston *et al.*, 2022) to produce estimates of second-order habitat selection
²⁵⁹ (Johnson, 1980). Quadrature points were determined using the raster cells in each animal's
²⁶⁰ 99.9% AKDE percentile and given a weight of 1. The number of quadrature locations greatly
²⁶¹ outnumbered the number of observed locations (Fig. B12), especially after accounting for
²⁶² the AKDE weights (Fig. B13).

263 Each species' model had the same structure:

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

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

276 4 Results

277 Overall, 2.6% of GPS locations had temperatures lower than -20°C , while 6.5% had temper-
278 atures above 20°C , and temperature ranges differed across species (Table 2, Fig. B2). At 0°C ,
279 species differed in overall mean probabilities of movement (range: 0.05 – 0.31), mean speed

280 when moving (range: 0.42 – 2.67 km/h), and mean distance traveled (i.e., $P(M) \times \mathbb{E}(S)$,
 281 range: 0.04 – 0.61 km/h; Table 3). Grizzly bears tended to move least often ($P(M) \approx 0.05$),
 282 while wolves and cougars moved most often ($P(M) \geq 0.22$). When moving, mountain goats
 283 and southern mountain caribou moved the slowest ($\mathbb{E}(S|M) \approx 0.43$ km/h), while wolves
 284 had the highest mean speed when moving ($\mathbb{E}(S|M) \approx 2.64$ km/h). Consequently, wolves
 285 traveled, on average, 0.6 km/h – 2.5 to 16.7 times further than other mammals at 0°C.

Table 2: Percentage of observed GPS locations (after data cleaning) with temperatures below -20°C or above 20°C.

Species	T < -20° C	T > +20° C
Canis lupus	1.7 %	13.0 %
Cervus canadensis	2.4 %	4.9 %
Oreamnos americanus	0.7 %	2.8 %
Puma concolor	0.7 %	6.9 %
Rangifer tarandus (boreal)	6.8 %	7.9 %
Rangifer tarandus (s. mountain)	1.3 %	3.4 %
Ursus arctos horribilis	0.0 %	8.4 %
Total	2.6 %	6.5 %

Table 3: Mean probability of movement ($P(M)$), speed ($\mathbb{E}(S)$, km/h, assuming constant movement), and distance travelled ($P(M) \times \mathbb{E}(S) = \mathbb{E}(D)$, km/h) as estimated by models without and with temperature ($\mathbb{E}(\dots|T)$), after post-stratification to a 1-hour sampling rate and a temperature of T = 0°C.

Species	$\hat{P}(M)$	$\hat{P}(M T)$	$\hat{\mathbb{E}}(S)$	$\hat{\mathbb{E}}(S T)$	$\hat{\mathbb{E}}(D)$	$\hat{\mathbb{E}}(D T)$
<i>C. canadensis</i>	0.16	0.17	0.57	0.57	0.09	0.10
<i>Canis lupus</i>	0.23	0.22	2.64	2.67	0.61	0.60
<i>O. americanus</i>	0.15	0.13	0.43	0.42	0.06	0.06
<i>Puma concolor</i>	0.27	0.31	0.74	0.76	0.20	0.24
<i>R. tarandus</i> (b)	0.19	0.18	0.71	0.73	0.14	0.13
<i>R. tarandus</i>	0.11	0.11	0.43	0.42	0.05	0.05
(sm)						

Species	$\hat{P}(M)$	$\hat{P}(M T)$	$\hat{\mathbb{E}}(S)$	$\hat{\mathbb{E}}(S T)$	$\hat{\mathbb{E}}(D)$	$\hat{\mathbb{E}}(D T)$
<i>U. arctos horr.</i>	0.05	0.05	0.72	0.72	0.04	0.04

Near 0°C, wolves selected for dense forest cover ($\gtrapprox 50\%$), elevations near 1 km, and distances from water < 10 km; elk selected for forest cover near 50%, elevations between 1 and 2 km, and distances from water of 5-15 km; mountain goats selected for sparse (< 50%) forest cover, elevations between 1 and 2 km; cougars selected for dense forest cover, an elevation of ~ 1 km, and distances from water < 10 km; boreal caribou selected for intermediate to dense forest cover, elevations near 500 m, and distances from water < 10 km; southern mountain caribou selected for dense forest cover, elevations near 2 km, and distances from water < 5 km; and grizzly bears selected for sparse forest cover (25-50%), elevation near 1 km, and distances from water < 2 km.

There was relatively strong agreement between models with and without temperature (Figs. B3, and B14), but including temperature always resulted in better fits. All analyses of deviance showed that temperature significantly affected movement behaviour (all p-values $< 2.2 \times 10^{-16}$; all $\Delta AIC \geq 342$; Table B2 and following pages in Appendix B). Accounting for temperature resulted in a simpler HRSF for mountain goats (lower model degrees of freedom) that fit the data better (lower deviance), and hence no test was necessary to show that the inclusion of temperature produced a better fit.

4.1 Effects of temperature on movement rates

The effects of temperature on movement rates varied in both direction and magnitude across species, even after accounting for differences in daily and seasonal activity (e.g., sleeping, migration, hibernation; Figs. B4-B6). Smooth interaction terms were well-behaved and indicated clear shifts in activity over time of day and day of year for all species. The models had good in-sample prediction (Fig. B7) and explained reasonably high proportions of the deviance (79.3% for the gamma model and 10.7% for the binomial model, which is relatively

309 high for a binomial model with binary responses: see ch. 11 of McElreath (2020)]. All
 310 species adapted their daily and seasonal movement behaviour to changes in temperature
 311 (Fig. 3). The clearest example of this was cougars. In mid summer, they moved mostly
 312 in the evening if temperatures were cool and mostly in the early morning if temperatures
 313 were hot. Throughout the year, they tended to move more when it was colder, but what
 314 they perceived as “colder” depended on the time of year. However, uncertainties around
 315 the estimated effects were often higher at extreme temperatures due to data scarcity. All
 316 species’ estimated probability of moving decreased with sampling intervals approximately
 317 above 1 hour, and most species’ estimated speed when moving decreased monotonically with
 318 sampling interval, although the estimated trends were highly uncertain for some species (Fig.
 319 B8).

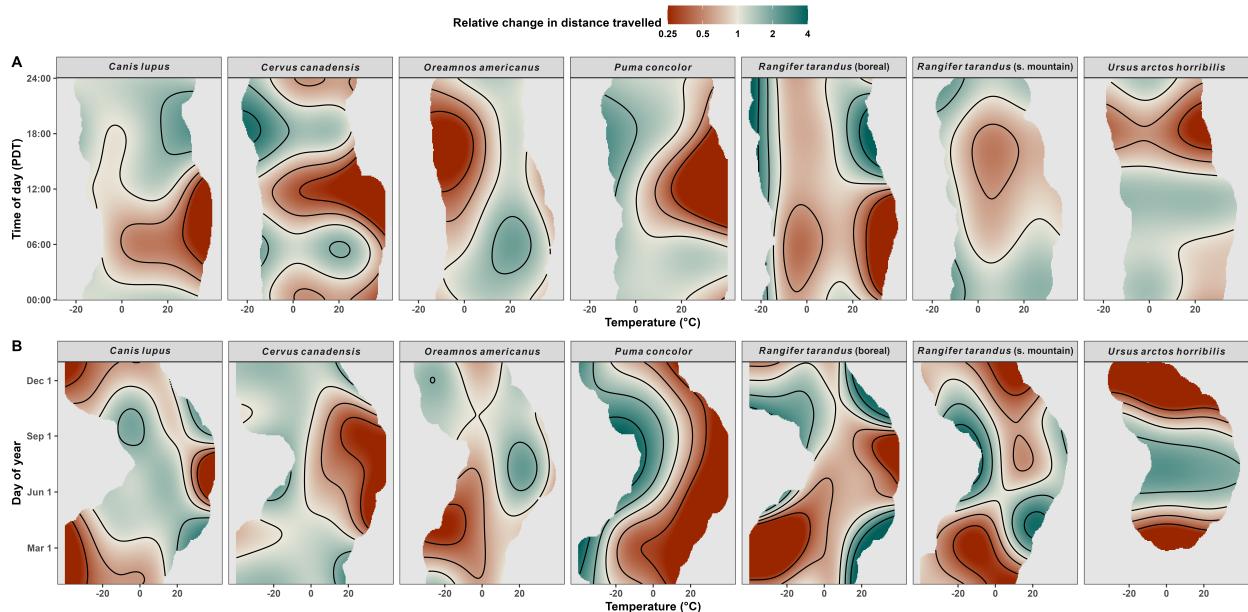


Figure 3: **Temperature is a strong determinant of how far and when mammals travel.** The fill indicates the estimated effects of temperature on the relative change in distance travelled (probability of moving times mean speed when moving) over time of day on June 1st (**A**) and day of year at 12:00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

320 4.2 Effects of temperature on habitat selection

321 Species’ relative selection strength (RSS) was generally strongest for elevation and weak-
 322 est for forest cover, but species’ RSS for resources depended on temperature (Fig. 4).

323 Changes in RSS with temperature were also strongest for elevation and generally weakest
 324 distance from water, but there were no common trends across all species for any of the
 325 three resources. All species, with the exception of cougars, exhibited a clear temperature-
 326 dependent shift in their preference for forest cover. At higher temperatures, wolves, mountain
 327 goats, and grizzly bears became less selective for forest cover, while elk and caribou shifted
 328 towards more intermediate forest cover without much of a change in preference width. All
 329 species shifted elevationally with temperature, although boreal caribou's selection strength
 330 for elevation was less sensitive to elevation. Overall, as temperatures rose, elk, mountain
 331 goats, and cougars increased in elevation, while boreal wolves, southern mountain caribou,
 332 and grizzly bears decreased in elevation. Most species generally remained within 5 km of
 333 water, and temperature did not affect their selection strength as much as for the other two
 334 resources. Again, estimated RSS values were generally most uncertain at extreme tempera-
 335 tures (Fig. B15).

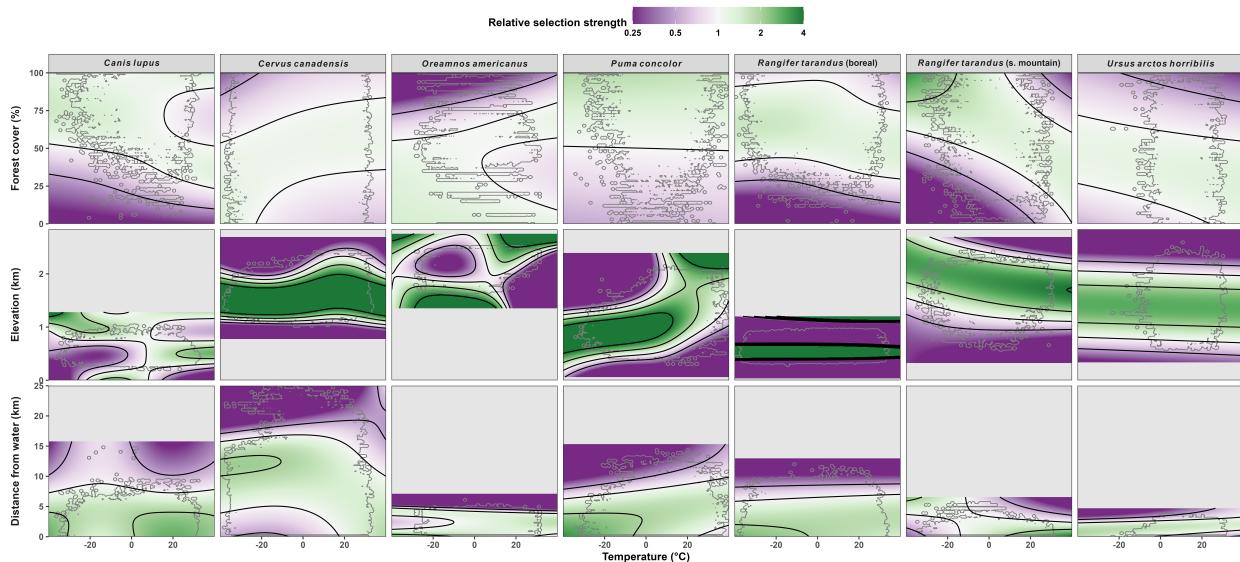


Figure 4: **Temeperature strongly affects mammals' habitat selection.** Estimated relative selection strength (RSS) for forest cover (%), elevation (km), and distance from water (km) as a function of temperature. The grey contours indicate the extent of each species' observed data. RSS values were re-centered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

336 4.3 Predicted changes in movement during the 21st century

337 The predicted changes in distance traveled varied across species in both direction and magni-
 338 tude, but worse climate-change SSPs always corresponded to greater absolute changes (Fig.

339 5). Additionally, species that were predicted to move less often did not necessarily have lower
 340 speeds when moving, and vice versa (Figs. B9 and B10). Overall, absolute changes by 2100
 341 under the best-case SSP were small (approximately 0% to +4%), while under the worst-case
 342 SSP absolute changes ranged from ~2% (grizzly bears) to ~24% (cougars). Notably, while
 343 the models estimated that grizzly bears would move substantially less (if at all) in winter
 344 (Figs. 3, B4-B6), the models did not explicitly account for changes in hibernation phenol-
 345 ogy. Consequently, the climate change projections do not explicitly account for changes in
 346 energetic needs or physiology. Projected changes also varied spatially due to heterogeneity
 347 in projected climate change (Fig. 6). Again, absolute changes were generally greatest under
 348 worse SSPs, but the direction of change at each location also varied across SSPs (most visible
 349 in cougars).

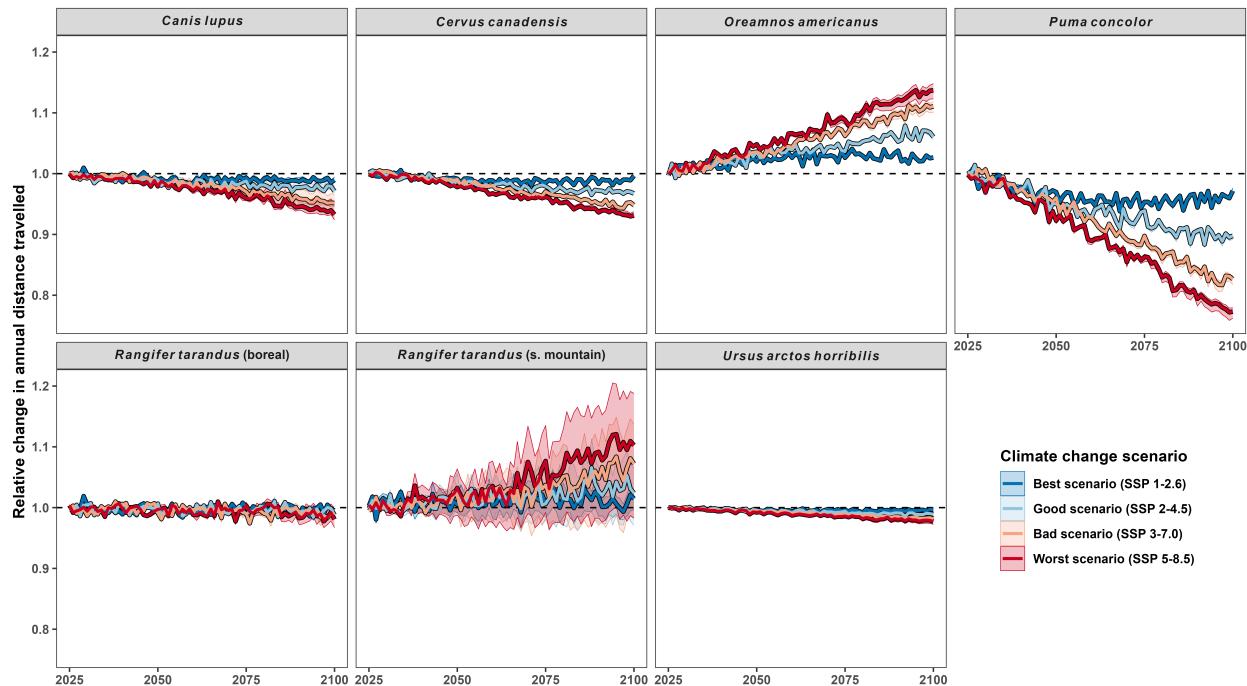


Figure 5: **The direction and magnitude of changes in movement rates due to climate change varies among species, but worse climate-change scenarios result in the greatest change.** Lines indicate the median projected change in distance travelled (probability of moving times speed when moving) due to changes in temperature within each species' observed extent. Shaded areas indicate the range of predicted values between the 95th and 5th percentiles. Changes are relative to the predicted mean distances travelled in 2025 across the four Shared Socioeconomic Pathways (SSPs). If the intervals are fully above the dashed line, at least 90% of the estimated means increased, relative to the each pixel's average of the four climate SSPs in 2025. Similar conclusions can be drawn regarding a decrease if the ribbons are below the dashed line. The projections only account for changes in movement behaviour (i.e., movement frequency and speed) and ignore changes in physiology or movement costs.

350 Median RSS was projected to decrease over time within the each species' observed range,

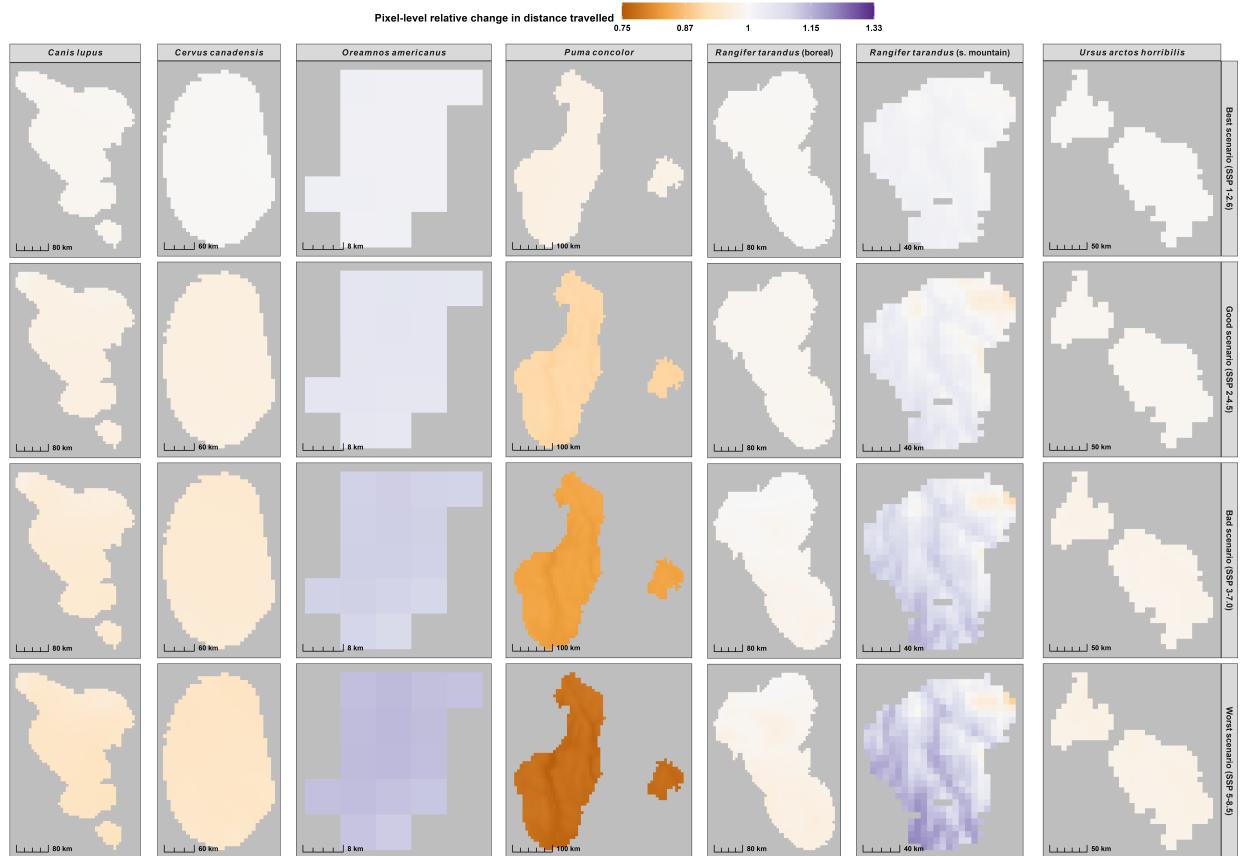


Figure 6: Climate change will impact each species' movement rates differently. The color scale indicates the predicted changes in distance traveled in 2100, relative to each pixel's average distance in 2025 across all four scenarios (i.e., not relative to other pixels). Values < 1 indicate a decrease, 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 0.67 and 1.5 ($\approx 2^{0.585}$; original data ranged 0.50 to 1.56). The predictions only account for the predicted temperature throughout the province and ignore environmental factors such as terrain slope, soil type, and forest density. All maps are shown with a BC Albers projection (EPSG:3005).

351 but changes were stronger under worse SSPs (Fig. 8). Decreases were most pronounced in
 352 the bottom fifth percentile and most severe for elk, southern mountain caribou, and mountain
 353 goats. Of all the species, only cougars showed a clear increase in RSS for areas within their
 354 current range. The change in RSS between 2025 and 2100 varied spatially for all species
 355 (Fig. 8). All species were predicted to exhibit a decrease in RSS throughout most of their
 356 observed habitats, although cougars were predicted to increase their selection for patches
 357 with higher altitude.

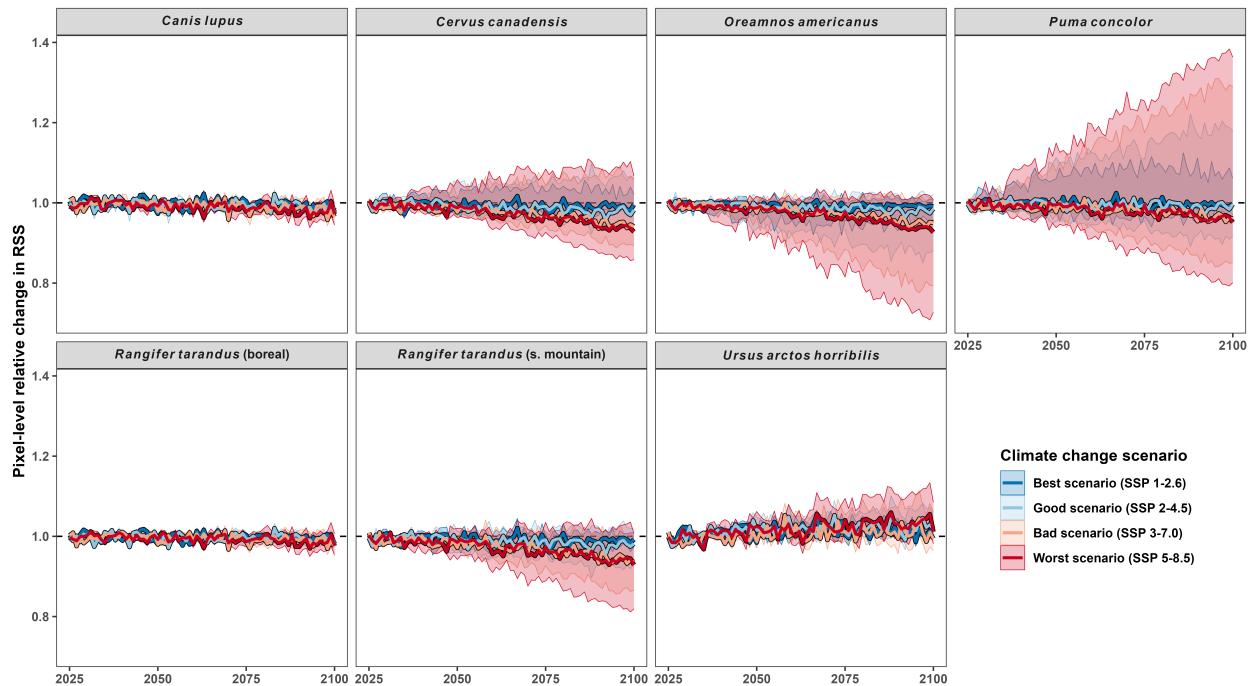


Figure 7: All species are expected to exhibit a decrease in median relative selection strength (RSS) for their current range, irrespective of climate change scenario, but decreases are stronger in the worse-case scenario. Lines indicate the projected change in median RSS within each species' observed extent within BC, while the ribbons indicate the range between the 95th and 5th percentiles in RSS. Changes are relative to each location's mean RSS in 2025 across the four Shared Socioeconomic Pathways (SSPs).

358 5 Discussion

359 We have demonstrated that temperature is an important determinant of whether, how,
 360 and where large mammals move, even while accounting for seasonality (e.g., changes in
 361 photoperiod, hormones, and resources). Disentangling temperature from other drivers is
 362 important for predicting how changes in climate will affect mammalian movement when

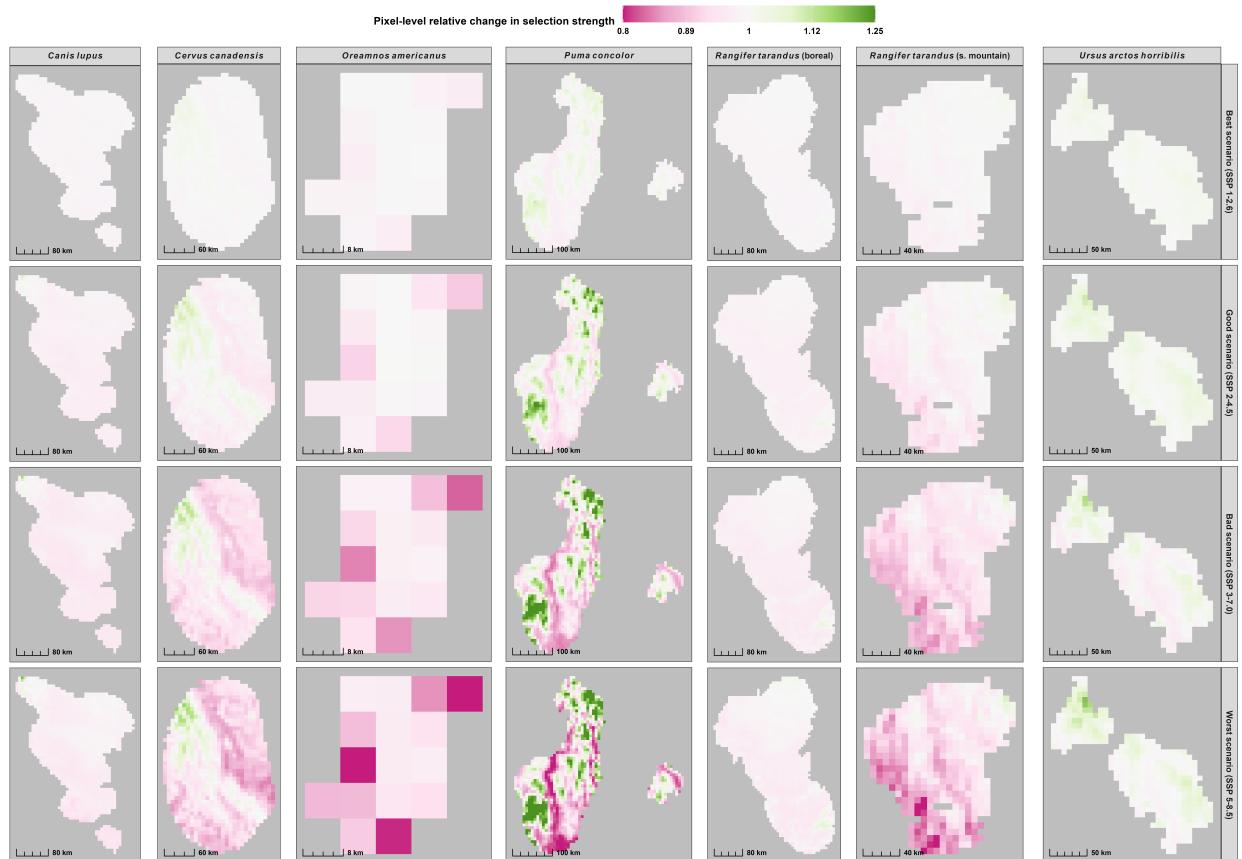


Figure 8: Climate change will impact each species' habitat relative selection strength (RSS) differently. The color scale indicates the predicted changes in RSS in 2100, relative to each location's average RSS in 2025 across all four scenarios (i.e., not relative to other pixels). Values < 1 indicate 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 0.67 and 1.5 ($\approx 2^{\pm 0.585}$; original data ranged 0.66 to 1.86). All maps are shown with a BC Albers projection (EPSG:3005).

363 other drivers remain approximately constant. However, predicting mammals' responses to
364 climate change becomes increasingly complex as habitats warm and animals are exposed to
365 increasingly frequent conditions that are both extreme and novel.

366 Predicting mammals' responses at the data-scarce fringes of the surface plots in Figs. 3
367 and 4 comes with substantial uncertainty, particularly given that the responses are nonlinear.
368 At warm temperatures, mammals (and other homeotherms) overheat (Alston *et al.*, 2020;
369 Dyer *et al.*, 2023), so their movement behaviour and that of their competitors, predators,
370 and/or prey can often be substantially different from the behaviour at typical temperatures.
371 As extreme temperature events become more frequent and prolonged throughout the year
372 (Yao *et al.*, 2022; IPCC, 2023), mammals will be increasingly forced towards atypical be-
373 haviours that may alter community structures and behaviours, both during such events and
374 afterwards (Logares & Nuñez, 2012; Anderson *et al.*, 2017; Zhang *et al.*, 2023). For instance,
375 changes in climate and phenology impact the life history and behaviour of many hibernat-
376 ing mammals (Wells *et al.*, 2022), and hot weather can also affects mammals' sleep quality
377 (Mortlock *et al.*, 2024) and likelihood to enter torpor (Fjelldal *et al.*, 2021).

378 Changes in animal movement behaviour may also alter the frequency and intensity of
379 human-wildlife conflict, especially with the addition of growing pressures from human de-
380 velopment and presence (Sih *et al.*, 2011; Johnson *et al.*, 2018; Weststrate *et al.*, 2024). At
381 the same time, warmer winters may reduce mammals' energetic expenditure (Berger *et al.*,
382 2018; Schmidt *et al.*, 2020), increase ease of movement as snow cover and depth decrease
383 (Leclerc *et al.*, 2021; Melin *et al.*, 2023), increase their chances of finding food or being
384 preyed on (Gilbert *et al.*, 2017; Hou *et al.*, 2020; Pedersen *et al.*, 2021; Slatyer *et al.*, 2022;
385 Sullender *et al.*, 2023), and affect the timing and duration of migrations (Sawyer *et al.*, 2009;
386 Leclerc *et al.*, 2021; Xu *et al.*, 2021). These changes will likely have complex consequences
387 for population and ecosystem structures and dynamics as prey, predators, and competitors
388 experience altered seasonal cycles and increasingly common climate "weirding" (Bunnell *et*
389 *al.*, 2011).

Our ability to respond changes in climate is contingent on our ability to prepare for and predict change. However, predicting animal behaviour becomes increasingly complicated as the conditions animals are exposed to deviate from current, typical conditions, especially when responses are nonlinear and data are sparse. Consequently, we do not present our results as a definitive guide to how mammals in western Canada will respond to climate change. Instead, we hope they serve as a starting point to (1) demonstrate that mammals' movement rates and habitat selection depend on temperature and (2) how one can estimate mammals' changes in movement behaviour due to climate change. Additionally, communicating uncertainty in one's estimates is crucial in assessing risk probabilistically, and appropriate measures of uncertainty require careful and robust modeling (Aven & Kvaløy, 2002; Ayre & Landis, 2012; Czado & Brechmann, 2014).

Achieving the “30 by 30” goal will require international collaboration (Huang & Zhai, 2021) as well as active partnership with local Peoples, especially Indigenous Peoples (Wong et al., 2020; Lamb et al., 2023). Understanding the consequences of climate change on mammals’ movement behaviour is a first step towards proactively responding to how mammals will respond to human-induced rapid environmental change (Sih et al., 2011; Williams & Blois, 2018). In the following sections, we discuss the implications of our results in more detail. We then expand on consequences for conservation during the 21st century and considerations for future studies.

5.1 Effects of temperature on movement rates

The heterogeneity mammals' responses to temperature suggests that ecological communities will respond to change in complex and interconnected ways. Although our models do not account for explicit physiological or phenological changes, the surfaces in Fig. 3 suggest that warmer temperatures cause many species to alter their daily and seasonal activity patterns (most visible in cougars and grizzly bears). For example, when temperatures were above 0°C, cougars moved most at night, but when temperatures were below 0°C they tended to move

more throughout the day. Throughout the year, they adapted their tolerance to temperature and moved less when it was relatively hot (for a given time of year), especially in spring and summer. The strong reduction in the mid-day movement rates of wolves, elk, cougars, and boreal caribou when summer temperatures were above 20°C suggests that the increasingly common and intense heat waves across western Canada will have community-wide impacts on movement rates, encounter rates, and potentially community structure (Martinez-Garcia *et al.*, 2020). More work is necessary on quantifying interspecific responses to temperature, including the effects of temperature on predation rates (but see: Cunningham *et al.*, 2021; Glass *et al.*, 2021; Brivio *et al.*, 2024). The increase in intensity and frequency of extreme heat events (Bunnell *et al.*, 2011; Yao *et al.*, 2022) will likely also impact the occurrence and timing of hibernation (Wells *et al.*, 2022) and migration or seasonal range expansions (Morley, 2021; Carbeck *et al.*, 2022; Malpeli, 2022). However, not all species may be able to adapt at the current rate of climate change (Heten *et al.*, 2014; Williams & Blois, 2018), especially since landscape changes will likely depend not only on the direct effect of temperature but also on cascading changes in the availability and unpredictability of resources (McLellan & McLellan, 2015; Pigeon *et al.*, 2016; Mezzini *et al.*, 2025).

5.2 Effects of temperature on habitat selection

As with the effects of temperature on movement rates, the heterogeneity of temperature effects on species' habitat selection indicates that efficient and proactive habitat conservation will require taxonomic nuance. In particular, our HRSFs did not account for any explicit physiological responses to temperature that may impact movement, such as changes in the phenology of plants, fire, ice, or mammalian physiology (e.g., moulting, fat storages) or behaviour (e.g., migration, food caching), other than as direct responses to temperature. Consequently, the behavioural changes we present should be interpreted carefully. While some seasonal cycles do not depend directly on temperature and may thus not be impacted directly by climate change (such as those driven by photoperiod, see Liu *et al.*, 2022), the

⁴⁴² predictions we present also rely on the assumption that mammals will not adapt these
⁴⁴³ seasonal cycles to temperature-dependent cues, such as weather (Xu & Si, 2019) or forage
⁴⁴⁴ availability (Middleton *et al.*, 2018), which may not be correct. Additionally, it is important
⁴⁴⁵ to stress the distinction between habitat selection and quality. While animals tend to select
⁴⁴⁶ for high-quality habitats (Kacelnik *et al.*, 1992; Wright, 2024), high selection strength can
⁴⁴⁷ also be a consequence of an ecological trap (Swearer *et al.*, 2021; Zuñiga-Palacios *et al.*,
⁴⁴⁸ 2021).

- ⁴⁴⁹ • geographic space *sensu* Matthiopoulos (2022)
⁴⁵⁰ • environmental space *sensu* Matthiopoulos (2022)
⁴⁵¹ • G space is the realization of the theoretical E space

⁴⁵² 5.3 Predicted changes in movement during the 21st century

⁴⁵³ Achieving the goals laid out by the “30 by 30” conservation initiative (Convention on
⁴⁵⁴ Biological Diversity, 2022) will require careful planning but often also rapid action. In the
⁴⁵⁵ case of Canada, only 13.7% of its terrestrial areas and inland waters were protected at the
⁴⁵⁶ end of 2023 (Environment and Climate Change Canada, 2024; Minister of Environment
⁴⁵⁷ and Climate Change, 2024). Additionally, efficient and effective conservation will require
⁴⁵⁸ collaboration with Indigenous and local communities to ensure Treaties are respected in the
⁴⁵⁹ process (Turner & Clifton, 2009; Wong *et al.*, 2020; Falardeau *et al.*, 2022; Lamb *et al.*,
⁴⁶⁰ 2023) while also actively preparing for future change (Desjardins *et al.*, 2020; Hessami *et al.*,
⁴⁶¹ 2021).

⁴⁶² The diversity in predicted changes in movement behaviour by 2100 (both across species
⁴⁶³ and within species’ current ranges) and high spatial heterogeneity in Fig. 8 highlight the
⁴⁶⁴ need for careful planning that incorporates not only reliable estimates of change but also
⁴⁶⁵ pragmatic and communicable measures of uncertainty and variability around such estimates.
⁴⁶⁶ For example, the width of the prediction intervals in Fig. 5 suggest that spatial and intra-
⁴⁶⁷ individual variation should be accounted for when deciding the location and size of protected

468 areas (Jeltsch *et al.*, 2025). Population-level means that ignore such variation can greatly
469 limit the efficacy of conservation projects (Muff *et al.*, 2020; Mortlock *et al.*, 2024; Silva
470 *et al.*, 2025). Additionally, accurate estimates of the effects of changes in temperature on
471 mammals' movement require a holistic view of the direct effects of temperature on mammals'
472 movement directly as well as its effects on other drivers of movement, such as forage and prey
473 availability (Mezzini *et al.*, 2025), encounter rates (Hou *et al.*, 2020; Martinez-Garcia *et al.*,
474 2020), population dynamics (Smith *et al.*, 2023), competitive pressure (Tórrez-Herrera *et al.*,
475 2020), and predation risk (Kohl *et al.*, 2019). This complexity results in the great variation
476 among the responses of different species (and individuals), especially as populations undergo
477 a rapid cascade of change (Botero *et al.*, 2015) and animals face increasing pressures from
478 human activity, including habitat fragmentation, habitat loss, and greater human presence
479 in wild spaces (Sawyer *et al.*, 2009; Sih *et al.*, 2011; Tucker *et al.*, 2018; Rice, 2022; Rosenthal
480 *et al.*, 2022; Weststrate *et al.*, 2024). As selection strength for current ranges changes (and
481 likely decreases), some animals may disperse, relocate to a new habitat, or remain within
482 the current range despite the reduced fitness and increased extinction risk (Duncan *et al.*,
483 2012; Logares & Nuñez, 2012; Anderson *et al.*, 2017).

484 **5.4 Species-specific considerations**

485 **5.4.1 *Canis lupus***

486 **5.4.2 *Cervus canadensis***

487 **5.4.3 *Oreamnos americanus***

488 **5.4.4 *Puma concolor***

489 attraction for disconnected patches of high elevation could lead to fragmentation or traps

490 **5.4.5 *Rangifer tarandus* (boreal)**

491 Increasing temperatures increased RSS for both elevations near ~500 m as well as > 1,000
492 m, but such a selection is only possible if: (1) such habitats exist in the animals' range, and
493 (2) crossing the 500 m to > 1,000 m regions is safe and attractive

494 **5.4.6 *Rangifer tarandus* (s. mountain)**

495 HRSFs do not account for migratory behaviour due to reproduction or predation risk

496 **5.4.7 *Ursus arctos horribilis***

497 **5.5 Considerations for future studies**

498 Our work highlights three central considerations for future research: (1) telemetry sam-
499 pling rates should be designed primarily in relation to the movement timescales of the species
500 of interest (Noonan *et al.*, 2019a; Nathan *et al.*, 2022; Pease, 2024), (2) the number of in-
501 dividuals tracked and the duration of each telemetry should depend not just on population
502 size but also the rate of environmental change, and (3) predicting changes in movement
503 behaviour becomes highly complex when responses are nonlinear, especially when changes
504 depend on many interacting factors (Polazzo *et al.*, 2024) and one is interested in predict-
505 ing responses in extreme conditions for which data are scarce (Steixner-Kumar & Gläscher,
506 2020).

507 While the `ctmm` movement models produced scale-independent estimates of speed (i.e.,
508 model interpretation is independent of sampling interval: Noonan *et al.*, 2019a), the accu-
509 racy, size, and stability of speed estimates still depended on the GPS sampling frequency.
510 This dependency is because coarsely-sampled movement data contains information on large-
511 scale movements (range crossings, migrations) but not fine-scale movements, including first-
512 order habitat selection (Johnson, 1980). Using the boreal caribou as an example, the 13-hour
513 sampling interval allows us to reasonably estimate the caribou's movement path at a tempo-

514 ral scale of approximately 13 hours (or greater), but we cannot produce reasonable movement
515 trajectories at a much finer (e.g., hourly) scale. Nathan *et al.* (2022) provides additional
516 examples of how the frequency of location data affects the results that can be inferred by
517 modeling movement behaviour. Consequently, we suggest being cautious when comparing
518 estimated movement behaviours across species, even though all predictions have been cor-
519 rected to the hourly timescale by predicting for 1-hour time intervals (i.e., `dt_hours = 1`).
520 Ideally, sampling schedules should be fine enough to reconstruct animals' movement move-
521 ment paths. Good estimates of an animal's speed and trajectory require telemetry locations
522 to be taken more often than the animal's directional persistence (Noonan *et al.*, 2019a), so
523 that, on average, the dataset contains multiple locations in between changes in direction.
524 What constitutes a change in direction depends on what movement scale one is investigating.
525 Small-scale movements and first-order spatial selection will require more frequent sampling
526 than migratory movement or second-order and third-order spatial selection. While `ctmm`
527 movement models are scale-invariant in that any model can be scaled to larger or smaller
528 areas and timescales, the model estimates are not independent of the scale of the sampling
529 frequency.

530 When landscapes are relatively predictable across years, a larger number of sampled
531 individuals is likely preferable over the duration of each tracking period. The greater number
532 of tracked animals allows one to quantify the variance across individuals, including the
533 range of conditions and environments that individual animals are in. A good estimate of
534 inter-individual variance provides better coefficient estimates along with more appropriate
535 measures of uncertainty. However, when conditions across years are stochastic, multi-year
536 telemetries allow one to better estimate inter-annual variation without conflating it with
537 inter-individual differences. Given the widespread, rapid, and accelerating changes across
538 many habitats (particularly at high elevations and at high latitudes), we suggest researchers
539 focus on long-term telemetry datasets to quantify the effects of intra-annual variability while
540 increasing the ranges of temperatures each individual is observed in. Longer observational

541 periods can also improve the chances of observing different community dynamics, such as
542 shifts in predator-prey dinamics.

543 Temperature affects many aspects of mammalian physiology and behaviour, including
544 energetics, sleep, and movement behaviour. Climatic changes during the last two centuries
545 have exposed many mammals to novel and increasingly extreme environmental conditions
546 that have led to visible changes that impact not only individuals but also ecological and
547 human communities. However, quantifying the effects of climate change is often complex,
548 especially as conditions become increasingly different and extreme events become increas-
549 ingly common. Accurately quantifying the nonlinear effects of temperature on when, how,
550 and where mammals move requires careful data collection and model design. We have pre-
551 sented a multi-species analysis of the effects of temperature on mammalian movement rates
552 and habitat selection in hopes that other researchers can leverage this framework and models
553 to expand our understanding of how temperature affects the movement behaviour of other
554 species, including smaller mammals, more elusive species, and non-mammal animals. Un-
555 derstanding of how temperature affects each species in a community will allow us to begin
556 making community-level inferences of how temperature will affect intra-specific interactions
557 from a movement behaviour perspective (Nathan *et al.*, 2008, 2022; Martinez-Garcia *et al.*,
558 2020). While adopting such a perspective is surely not simple, it would result in more com-
559 plete estimates of the effects of climate change on community ecology, particularly when
560 species are exposed to rapid change in many important variables. Future work should ex-
561 plore the effects of temperature on movement behaviour while accounting for finer-scale and
562 species specific variables that were not accounted for in this study. Examples of these include
563 temporally dynamic measures of forest type and age, canopy density, competitive pressures,
564 forage availability, and predator avoidance, or environmental stochasticity. However, many
565 of these data not available, so we also suggest that more work be done on quantifying such
566 measures using spatiotemporally dynamic models and sufficiently fine resolutions.

⁵⁶⁷ **6 Author contributions**

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

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