

Predicting how climate change will affect terrestrial mammals' movement and habitat selection in British Columbia, Canada

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Article type: Research article

Words in abstract: 133

Words in main text: 2470

Figures: 7

Tables: 1

References: 38 (updated on 2024-07-28)

Appendices: 3

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

Abstract

Recent widespread warming has caused many terrestrial mammals to change when, how, and where they move. These changes in species' movement behavior have had cascading effects on individuals' fitness and habitat selection with consequences at the population, community, and ecosystem levels. Previous research has quantified changes in mammalian movement behavior, but we are lacking an estimate of the effects of climate change on fine-scale movement and habitat selection. We address this by using Continuous-Time Movement Models and Hierarchical Generalized Additive Models to quantify the effects of temperature on mammal's probability of movement, speed, and habitat selection. We then leverage the estimated effects to predict when, how, and where mammals will move in BC in the current century. We conclude with implications for energetics, encounter rates, habitat conservation, and human-wildlife conflicts.

Useful references to add

- Hegel *et al.* (2010): weather affects caribou calf recruitment and interacts with predator (wolf) abundance
- Elmore *et al.* (2017): “thermal environments should be foundational in the understanding of the habitat concept”
- Pease (2024): the scale at which we measure variables affects their estumated effect
- Hetem *et al.* (2014):
 - rate of climate change is too fast for genetic adaptation to occur in mammals with longevities of decades
 - example of suitable habitat prediction to 2050
 - to read: <https://doi.org/10.1186/s40665-016-0024-1>

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¹ 1 Introduction

² It is well understood that mammalian energetics depend on ambient temperature (Taylor,
³ Heglund & Maloiy, 1982; Brown *et al.*, 2004), but we have a limited understanding of how
⁴ mammals adapt their movement behavior in response to temperature (Elmore *et al.*, 2017;
⁵ but see: Milling *et al.*, 2017; Montgomery *et al.*, 2019). Previous work has focused on
⁶ energetic costs of movement (Taylor *et al.*, 1982; Dyer *et al.*, 2023), range shifts (Leclerc *et*
⁷ *al.*, 2021), thermoregulation (Mota-Rojas *et al.*, 2021; Melin *et al.*, 2023), and trait-based
⁸ responses (McCain, 2019), but there remains a need for a more comprehensive understanding
⁹ of how mammals will adapt their fine-scale movement and habitat selection to future changes
¹⁰ in temperature (Intergovernmental Panel On Climate Change, 2023). Movement plasticity
¹¹ (Nathan *et al.*, 2008) allows mammals to react to changes in temperature on a shorter
¹² timescale than evolutionary physiological adaptations (Levins, 1974). By changing when,
¹³ how, and where they move, mammals can conserve chemical and thermal energy as well
¹⁴ as reduce the risk of overheating (Attias *et al.*, 2018; Williams & Blois, 2018; Alston *et*
¹⁵ *al.*, 2020; Verzuh *et al.*, 2023; Dyer *et al.*, 2023; Giroux *et al.*, 2023). We present a multi-
¹⁶ species analysis of how mammals adapt their movement behavior in response to changes in
¹⁷ air temperature.

¹⁸ Recent changes in climate have affected mammals' movement rates and habitat selection
¹⁹ (Deb, Forbes & MacLean, 2020), but it is still unclear how changes in the current century will
²⁰ affect their fine-scale movement behavior and spatial distribution by the end of the century.
²¹ In the last 200 years, many ecosystems experienced widespread warming that resulted in
²² milder and shorter winters, hotter and longer summers, and a greater risk of extremely high
²³ temperatures and severe forest fires (Zurowski, 2023; Intergovernmental Panel On Climate
²⁴ Change, 2023). Over the next 100 years, these changes will continue to affect mammals'
²⁵ fitness, movement behavior, and habitat selection as they cope with growing heat stress
²⁶ (Deb *et al.*, 2020; Woo-Durand *et al.*, 2020) and frequency and intensity of extreme events

27 (Bunnell, Kremsater & Wells, 2011) along with anthropogenic pressure (Sih, Ferrari & Harris,
28 2011; Weststrate *et al.*, 2024).

29 Understanding animals' responses to temperature is essential for anticipating their re-
30 sponse to climate change in the coming decades and the cascade of consequences such changes
31 will have. In light of the "30 by 30" conservation initiative, a global effort to conserve 30%
32 of the world's lands and oceans by 2030 ([ref?](#)), we must understand which areas are best
33 preserved to maximize the project's effectiveness. Predicting how climate change will affect
34 how, when, and where animals will move is necessary for choosing which 30% of the world
35 is most worth preserving. Changes in movement behavior impact several aspects of animals'
36 fitness, behavior, and odds of survival, including encounter rates (with food, competitors,
37 and predators: Martinez-Garcia *et al.*, 2020), energetic expenditure (Taylor *et al.*, 1982),
38 range shifts (Woo-Durand *et al.*, 2020). Thus, understanding the effects of temperature on
39 animals' movement behavior and their consequences is crucial for effective conservation.

40 This paper provides an analysis of the effects of ambient temperature on the movement
41 of six terrestrial mammal species in British Columbia (BC), Canada (*Canis lupus*, *Cervus*
42 *canadensis*, *Oreamnos americanus*, *Puma concolor*, boreal and southern mountain *Rangifer*
43 *tarandus*, and *Ursus arctos horribilis*; Table 1). Using over two decades of telemetry data
44 over a large spatial range of British Columbia (Fig. 1) and hourly weather data, we estimate
45 how mammals altered their movement frequency, movement speed, and habitat selection in
46 response to air temperature. We then pair the estimated responses with climate change
47 projections to forecast changes in mammalian movement in 2100 under different climate-
48 change scenarios (Shared Socioeconomic Pathways, see Riahi *et al.*, 2017). We discuss the
49 consequences of these changes in movement behavior with regards to energetics, encounter
50 rates, habitat conservation, and human-wildlife conflicts.

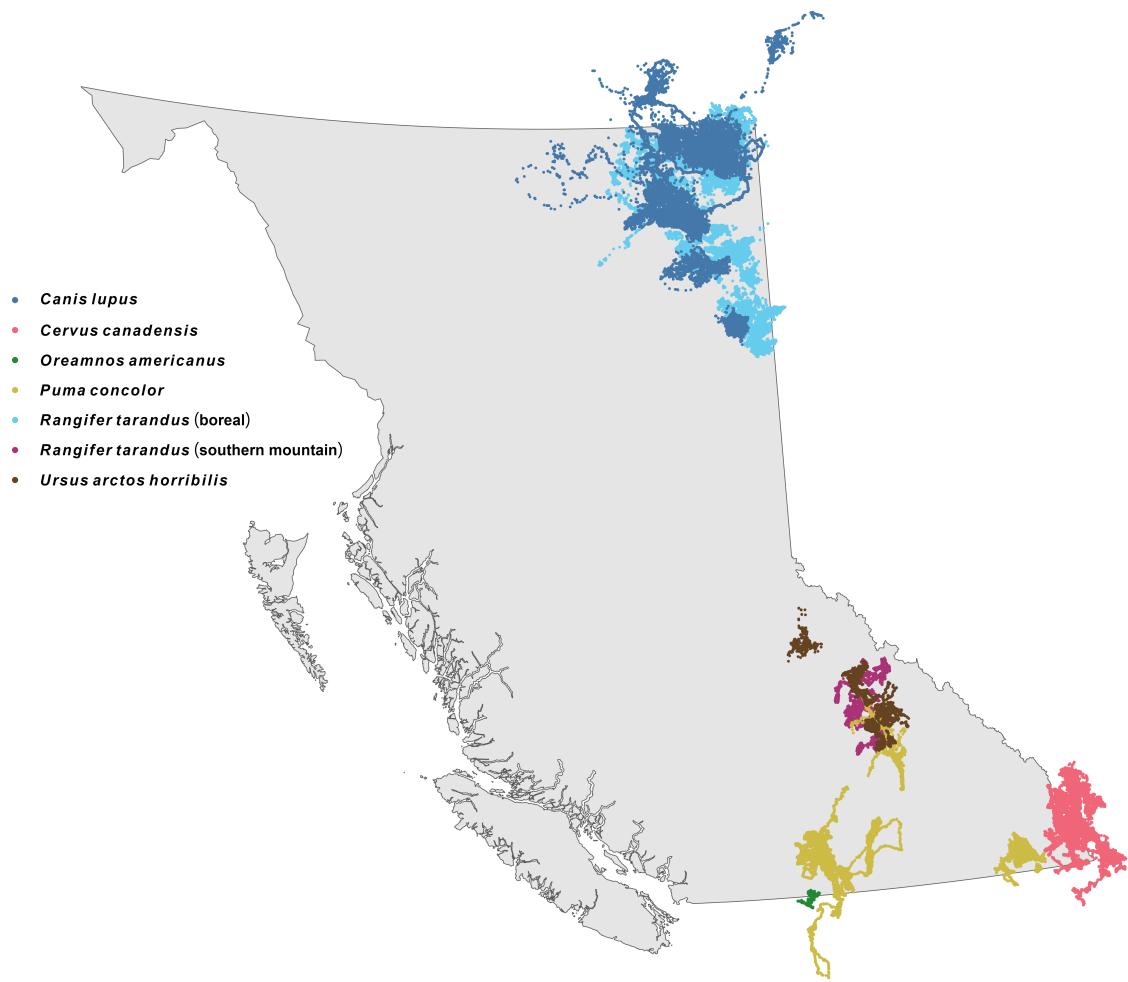


Figure 1: GPS telemetry data and 95% autocorrelated kernel density utilization distributions for the six species in this study.

Table 1: Start and end of the GPS telemetries along with the median sampling interval (Δt) for each of the species in this study.

Dataset	Start	End	Median Δt (hours)
<i>Canis lupus</i>	2013-01-27	2017-08-29	0.25
<i>Cervus canadensis</i>	2007-01-13	2013-11-20	2.00
<i>Oreamnos americanus</i>	2019-06-25	2023-10-05	6.24
<i>Puma concolor</i>	2006-02-05	2021-07-13	2.00
<i>Rangifer tarandus</i> (boreal)	2011-03-02	2018-01-04	12.99
<i>Rangifer tarandus</i> (southern mountain)	1998-03-21	2009-06-07	5.98
<i>Ursus arctos horribilis</i>	2004-09-30	2009-09-07	1.00

51 2 Methods

52 2.1 GPS telemetry data

53 Elk (*Cervus canadensis*) data from Ciuti *et al.* (2012) were downloaded from Movebank
 54 (study name: Elk in southwestern Alberta, see Kays *et al.*, 2022), while boreal caribou
 55 (*Rangifer tarandus*) and wolf (*Canis lupus*) telemetries were acquired via a public BC Oil and
 56 Gas Research and Innovation Society repository (<https://www.bccogris.ca/projects/boreal->
 57 caribou-telemetry-data), and the mountain goat (*Oreamnos americanus*) locations were pro-
 58 vided by BC Parks. All other tracking data were obtained from private collaborators. Outlier
 59 GPS locations were removed following diagnostic analyses of the distance from the median
 60 location as well as straight-line displacement, turning angle, and time interval between con-
 61 secutive points. Particular attention was paid to points with large turning angles ($\gtrapprox 170^\circ$)
 62 and high straight-line displacement, especially if antecedent and subsequent points indicated
 63 stationary behavior. The script used to clean the data and all custom functions used are avail-
 64 able on GitHub (<https://github.com/QuantitativeEcologyLab/bc-mammals-temperature>).

65 **2.2 Historical temperature data**

66 Rasters of hourly reanalyzed air temperature data were downloaded from the ERA5 dataset
67 (Hersbach *et al.*, 2023) from the European Center for Medium-range Weather Forecast-
68 ing server (ECMWF; www.ecmwf.int; <https://cds.climate.copernicus.eu>). Proximal weather
69 conditions were estimated for each location by extracting the values from the corresponding
70 raster cell from the temporally nearest raster using the `extract()` function from the `terra`
71 package (version 1.7-46, Hijmans, 2023) for `R` (R Core Team, 2024).

72 **2.3 Estimating mammals' instantaneous speeds**

73 We modeled each animal's movement using continuous-time movement models (Fleming *et*
74 *al.*, 2014) via the `ctmm` package (version 1.2.0, Fleming & Calabrese, 2023) for `R`. We then
75 estimated mammals' instantaneous speeds by applying the `ctmm::speeds()` function on all
76 models with finite speed estimates (416 of 433, see Fleming *et al.*, 2014; Noonan *et al.*,
77 2019). The 17 telemtries with insufficiently fine sampling were for caribou (15 boreal and
78 2 southern mountain; see Table 1).

79 Since `ctmm`'s movement models assume stochastic but non-zero speeds (i.e., a single,
80 stochastic moving state), data-informed speeds needed to be corrected so that the minimum
81 instantaneous speed could be 0. We performed this correction by subtracting the data-
82 independent, background minimum speed while assuming speeds were χ^2 -distributed and
83 correcting the degrees of freedom and confidence intervals accordingly. The function we
84 used is available on GitHub at <https://github.com/QuantitativeEcologyLab/bc-mammals->
85 [temperature/blob/main/functions/detrend_speeds.R](https://github.com/QuantitativeEcologyLab/bc-mammals-temperature/blob/main/functions/detrend_speeds.R). To avoid artifacts due to excessively
86 small, non-zero speeds, we determined whether an animal was moving or not using the
87 inflection point of each species' histogram of detrended speed estimates (Appendix A).

88 **2.4 Estimating the effects of temperature on mammals' movement**

89 **2.4.1 Movement frequency and speed**

90 We estimated the effects of temperature on mammals' state (moving or not) and speed
91 (given the animal was moving) using two Hierarchical Generalized Additive Models (HGAMs,
92 see Pedersen *et al.*, 2019) with the `mgcv` package for R (version 1.9-1, Wood, 2017). The
93 first HGAM estimated the probability that an animal was moving with a binomial fam-
94 ily of distributions. The second HGAM estimated an animal's speed (given that it was
95 moving) with a gamma Location-Scale family of distributions (`mgcv::gammals()`, Wood,
96 Pya & Säfken, 2016). Unlike the more commonly used gamma family (`stats::Gamma()`),
97 the `mgcv::gammals()` family allows the mean-variance relationship to depend on covariates
98 rather than assuming a constant mean-variance relationship. For example, if mean speed
99 increases with temperature but the scale decreases, the variance in speed will not increase
100 as much as with a constant scale parameter. The animal would then have low average speed
101 but a (relatively) large variance at cold temperatures, and a high average speed with a
102 (relatively) small variance at high temperatures.

103 The binomial and gamma HGAMs (see code chunk below) included random intercepts
104 for each animal (`s(..., bs = 're')`), fixed intercepts for each species, and factor smooth
105 interactions for time of day, day of year, and temperature for each species (`s(..., bs =`
106 '`fs`'), see model S in Figure 4 of Pedersen *et al.*, 2019). Additionally, the models had
107 three tensor product interaction terms (`mgcv::ti()`) for each species: (1) day of year and
108 time of day, (2) temperature and time of day, and (3) temperature and day of year. These
109 three terms accounted for: (1) seasonal changes in day length, (2) changes in the response
110 to temperature at the hourly scale (e.g., changes in nocturnality), and (3) seasonal changes
111 in the response to temperature (e.g., due to differences in coats), including changes in the
112 timing of migratory behavior. The HGAMs accounted for the cyclicity of time of day and
113 day of year using cyclic cubic splines (`bs = 'cc'`, Wood, 2017). Together, the binomial

- ¹¹⁴ HGAM and the gamma HGAM inform us on an animal's long-term average speed, since it
¹¹⁵ is the product of the probability the animal is moving and its average speed when moving.
¹¹⁶ Additional details are provided in Appendix A.

```
m_1 <- bam(
  moving ~
    s(animal, bs = 're') +
    species +
    s(tod_pdt, by = species, k = 5, bs = 'cc') +
    s(doy, by = species, k = 5, bs = 'cc') +
    s(temp_c, by = species, k = 5, bs = 'tp') +
    ti(doy, tod_pdt, by = species, k = 5, bs = c('cc', 'cc')) +
    ti(temp_c, tod_pdt, by = species, k = 5, bs = c('tp', 'cc')) +
    ti(temp_c, doy, by = species, k = 5, bs = c('tp', 'cc')) +
    s(log(dt), k = 3) +
    s(log(dt), species, k = 3, bs = 'fs'),
  data = d,
  method = 'fREML', # fast REML
  discrete = TRUE, # discretize the covariates for faster computation
  knots = list(tod_pdt = c(0, 1), doy = c(0.5, 366.5))) # for bs = 'cc'

m_2 <- bam(
  speed_est ~
    s(animal, bs = 're') +
    species +
    s(tod_pdt, by = species, k = 5, bs = 'cc') +
    s(doy, by = species, k = 5, bs = 'cc') +
    s(temp_c, by = species, k = 5, bs = 'tp') +
    ti(doy, tod_pdt, by = species, k = 5, bs = c('cc', 'cc')) +
    ti(temp_c, tod_pdt, by = species, k = 5, bs = c('tp', 'cc')) +
    ti(temp_c, doy, by = species, k = 5, bs = c('tp', 'cc')) +
    s(log(dt), k = 3) +
    s(log(dt), species, k = 3, bs = 'fs'),
  family = Gamma(link = 'log'),
  data = d_2, # data filtered for speed > 0
  method = 'fREML',
  discrete = TRUE,
  knots = list(tod_pdt = c(0, 1), doy = c(0.5, 366.5)))
```

¹¹⁷ 2.4.2 Habitat selection

- ¹¹⁸ We estimated the effects of temperature on each species' selection for percent forest cover,
¹¹⁹ elevation, and distance from fresh water (i.e., not sea water) using a series of HGAMs with

120 Poisson families of distributions (Appendix B, also see Aarts *et al.*, 2008; Alston *et al.*, 2022).
 121 While we recognize there are other important drivers of habitat selection, we decided to only
 122 use these three proxies to produce results that are relatively comparable between species and
 123 to make province-wide predictions simpler. Each species' model had the same structure:

```

rsf <- bam(
  detected ~ # 1 for GPS locations, 0 for quadrature data
  # species-level average resource preference
  s(forest_perc, k = 6, bs = 'tp') +
  s(elevation_m, k = 6, bs = 'tp') +
  s(dist_water_m, k = 6, bs = 'tp') +
  # animal-level deviations from the species-level average
  s(animal, bs = 're') +
  s(forest_perc, animal, k = 6, bs = 'fs', xt = list(bc = 'cr')) +
  s(elevation_m, animal, k = 6, bs = 'fs', xt = list(bc = 'cr')) +
  s(dist_water_m, animal, k = 6, bs = 'fs', xt = list(bc = 'cr')) +
  # changes in preference with temperature
  ti(forest_perc, temperature_C, k = 4, bs = 'cr') +
  ti(elevation_m, temperature_C, k = 4, bs = 'cr') +
  ti(dist_water_m, temperature_C, k = 4, bs = 'cr'),
  family = poisson(link = 'log'),
  data = d,
  weights = weight, # based on AKDE
  method = 'fREML',
  discrete = TRUE)
  
```

124 Smooth effects of forest cover, elevation, and distance to fresh water accounted for the
 125 species-level average selection strength for each resource. A random effect for each individual
 126 animal corrected for uneven sampling across individuals, while factor smooth interaction
 127 terms (`bs = 'fs'`) accounted for individual level resource selection (i.e., individual-level
 128 deviations from the species-level average). Finally, tensor interaction product terms (`ti()`) of
 129 each resource and temperature estimated the effect of temperature on the selection strength
 130 for each resource. Each model used a Poisson distribution and a log link function because
 131 detected is the number of animals (0 or 1) within a small, finite amount of space and
 132 time. Detections were down-weighted proportionally to their dependence on temporally
 133 proximate detections (see Appendix C and Alston *et al.*, 2022), while quadrature points
 134 had a weight of 1. Finally, we fit each model with fast REML ('`fREML`') and discretized

135 covariates (`discrete = TRUE`) to optimize computational efficiency with no meaningful
136 losses to model performance (Wood, Goude & Shaw, 2015; Wood *et al.*, 2017; Li & Wood,
137 2020).

138 **2.5 Predicting changes in animal movement during the current century**

139 *check this*

140 Rasters of projected monthly average temperature in BC from 2020 to 2100 were obtained via
141 the `climatenar` package (version 1.0, Burnett, 2023) for R. Since the climate projections did
142 not provide a measure of variation in temperature within each month, we estimated within-
143 month variance by fitting a GAM for location and scale (GAMLS, see Rigby & Stasinopoulos,
144 2005; Stasinopoulos & Rigby, 2007) to the monthly variance in temperature using the hourly
145 ERA5 data for BC during from 1998 to 2023 (extremes included, see Hersbach *et al.*, 2023).
146 The model included smooth terms of the monthly mean temperature, month, and year as
147 well as and a two-dimensional smooth of space and a tensor interaction product term of
148 space and month (Appendix C).

149 We accounted for hourly variation in weather by assuming temperature followed a normal
150 distribution with mean specified by the `climatenar` climate projectionS and variance as
151 specified by the Gamma GAMLS. We then predicted changes in movement behavior and
152 habitat selection as a function of temperature using the HGAMs and HRSFs along with the
153 temperature HGAM described above. For each month within each year from 2020 to 2100
154 we simulated hourly weather by including temperatures from the 5%, 10%, 20%, ..., 80%,
155 90%, and 95% (?) quantiles and weighted each quantile proportionally to the Gaussian
156 probability density for each value (Appendix C).

157 **3 Results**

158 **3.1 Effects of temperature on movement rates**

159 Partial effect of temperature varied across species (Fig. **AX**), even after accounting for
 160 differences in daily and seasonal activity (e.g., sleeping, migration, hibernation; see Fig.
 161 **AX**). Smooth interaction terms were well-behaved and indicated clear shifts in daily activity
 162 for all species. The models explained reasonably high proportions of the deviance (11% for
 163 the binomial model and 79% for the Gamma model) and had good in-sample prediction (Fig.
 164 **AX**).

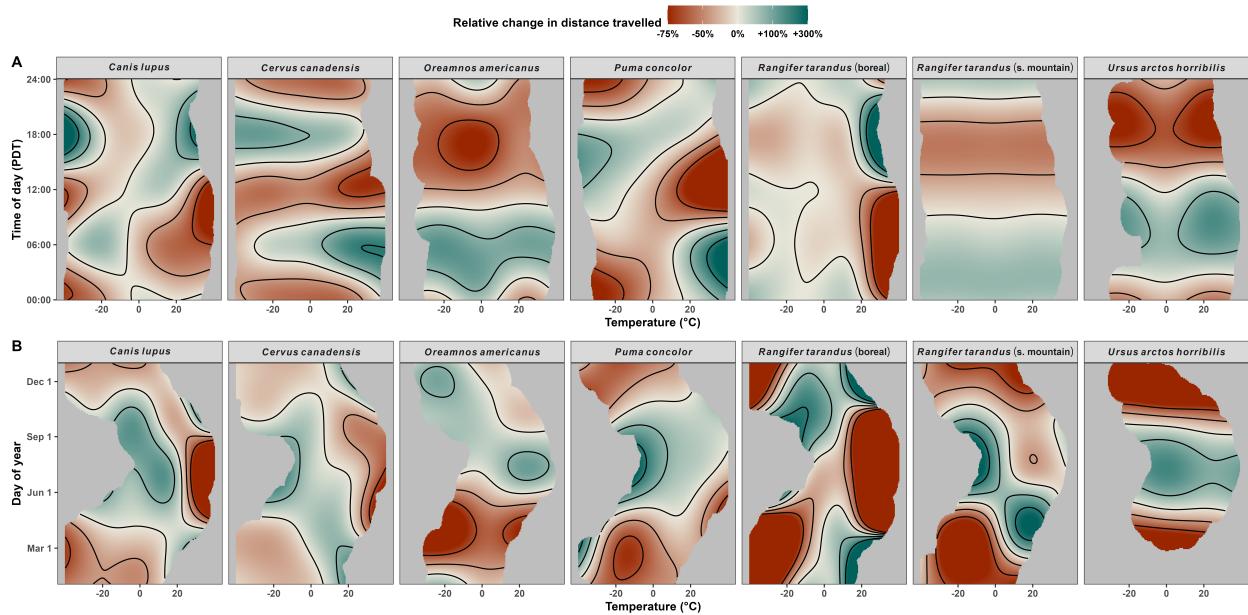


Figure 2: **Temperature is a strong determinant of how far and when mammals' travel.** Estimated effects of temperature on relative change in distance travelled (probability of moving times speed when moving) over time of day (**A**) and day of year (**B**). Predictions in the surface plots extend to 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 -75% and +300% for ease of readability.

165 Both movement frequency and speed when moving decreased with increasing sampling
 166 interval, with a strong common effect (Fig. **AX**). *here*
 167 `ctmm` models are scale independent assuming single, homogeneous behavior, but scale-
 168 dependency in the behavior (data) causes sampling effects
 169 worse climate-change scenarios corresponded to greater changes in behavior along with
 170 greater variance in within years

¹⁷¹ 3.1.1 Predicted changes in movement during the current century

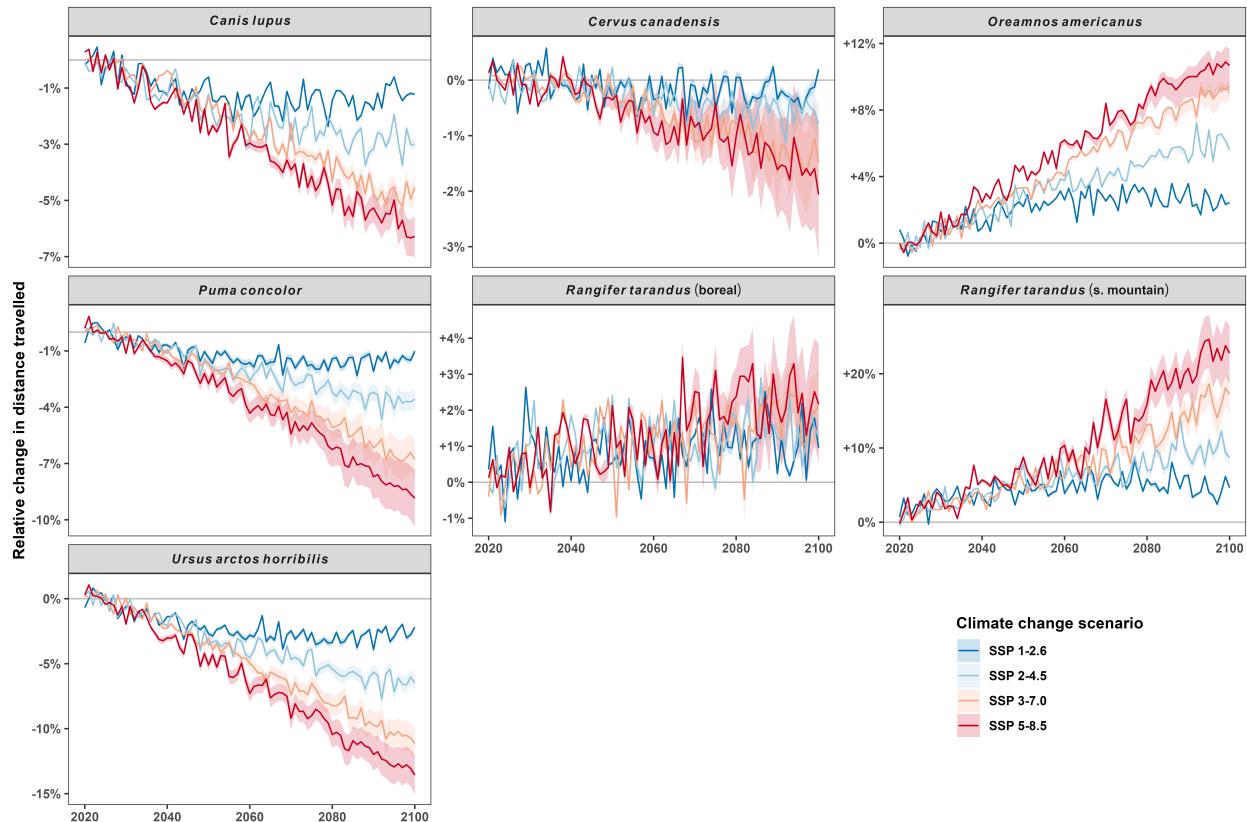
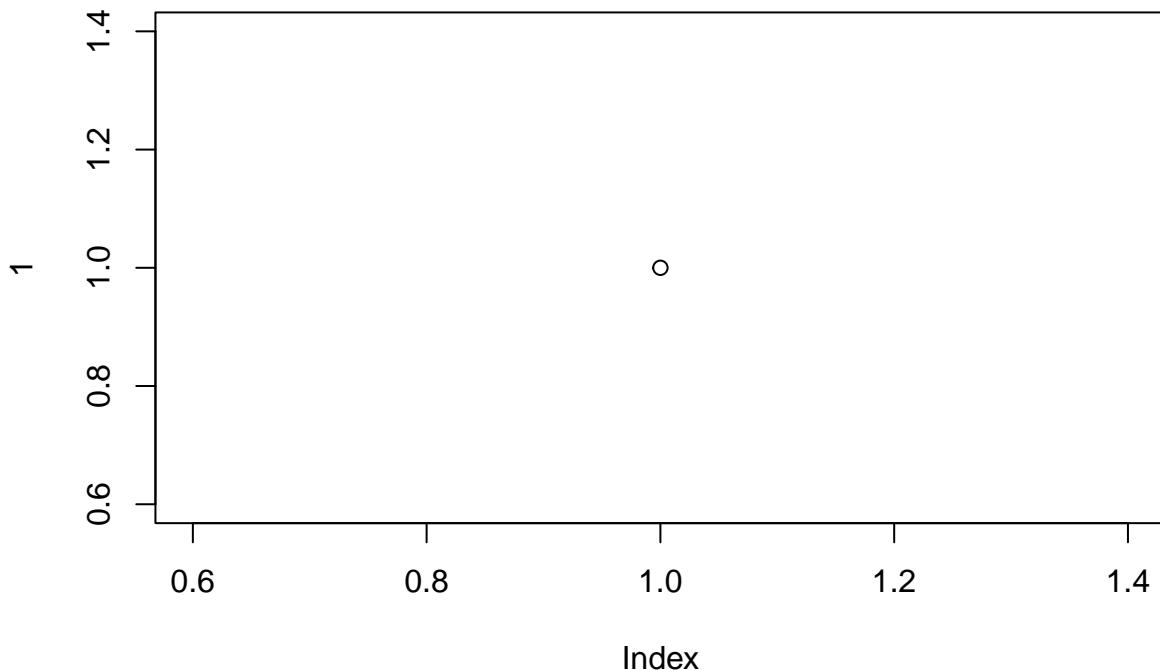


Figure 3: The intensity and direction of changes in movement rates due to climate change vary among species, but worse climate-change scenarios consistently result in the greatest change and greatest uncertainty. Lines indicate the projected relative change in mean distance travelled (probability of moving times speed when moving) due to changes in temperature within the species' current extent. Shaded areas indicate the mean 95% Bayesian credible intervals. Changes are relative to the mean distances travelled in 2020 across the four Shared Socioeconomic Pathways (SSPs). The SSPs are listed in order of similarity to current conditions, from SSP 1-2.6 (sustainability, best-case scenario) to 5-8.5 (fossil-fueled development, worst-case scenario). The projections only account for changes in movement behavior (i.e., movement frequency and speed) and ignore changes in physiology or movement costs.

4. spatial projections of distance in 2020 and 2100



172

173 3.2 Effects of temperature on habitat selection

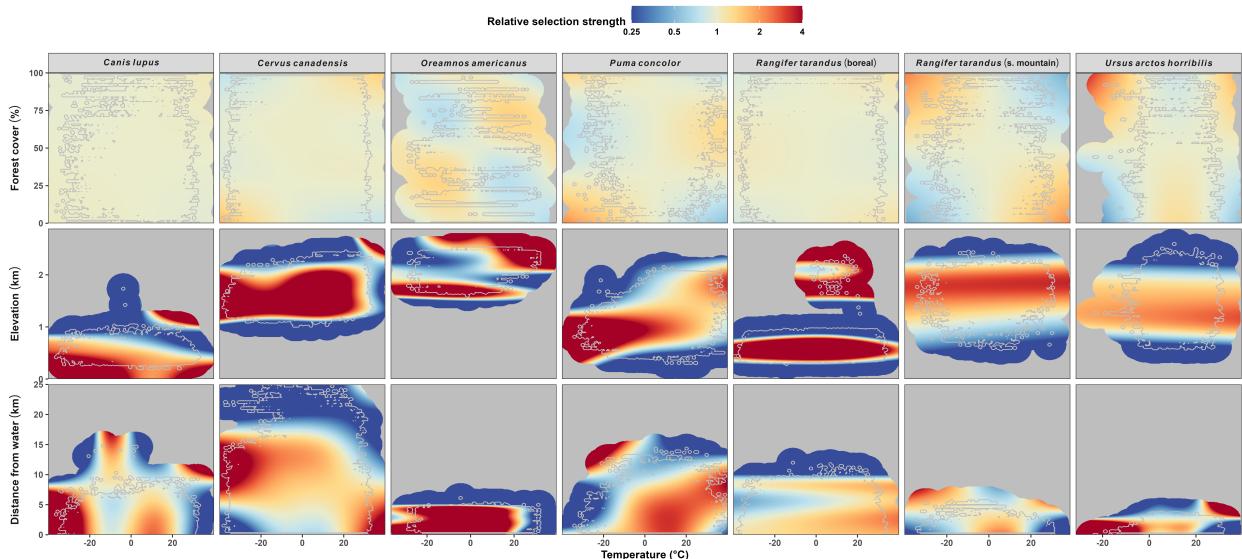


Figure 4: **Central message.** Estimated resource selection strength for forest cover (%), elevation (km), and distance from fresh water (km) as a function of temperature. The grey contours indicate the extent of each species' observed locations.

¹⁷⁴ 3.2.1 Predicted changes in movement during the current century

6. temporal projections of RSFs within current area

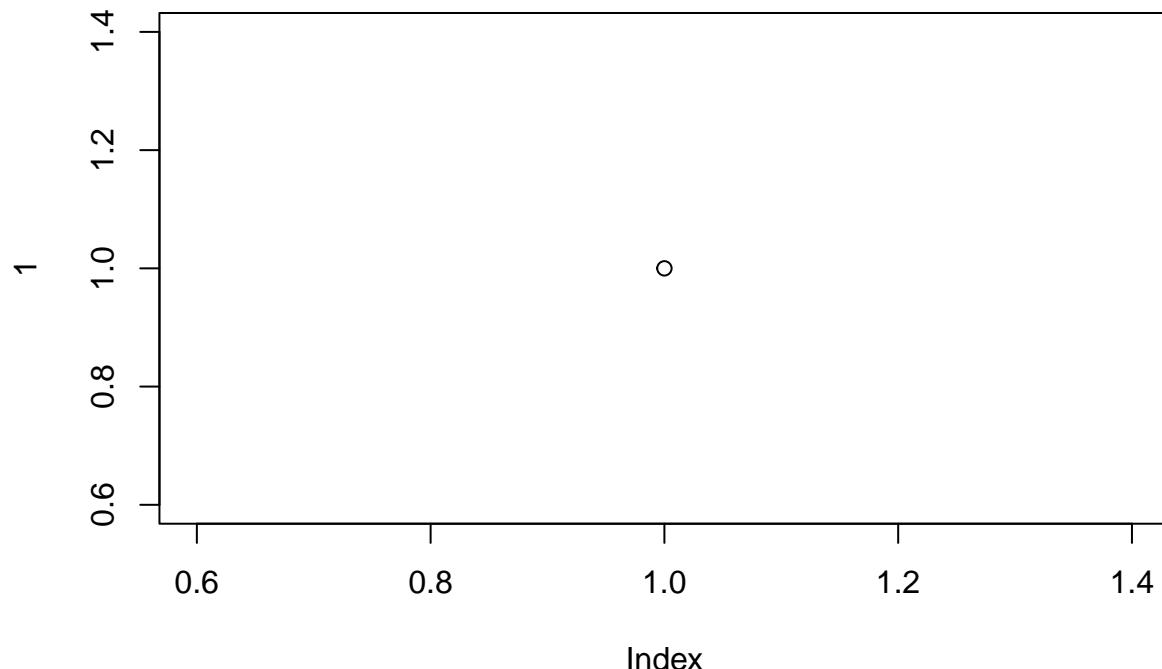
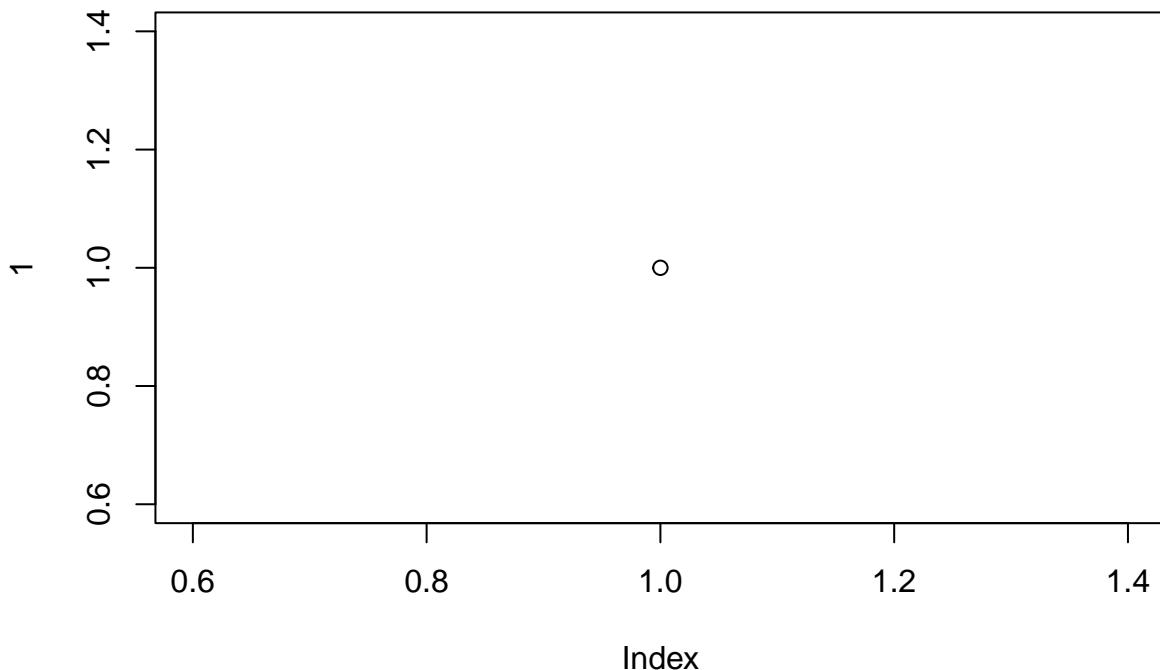


Figure 5: The intensity and direction of changes in habitat selection due to climate change vary among species, but worse climate-change scenarios consistently result in the greatest change and greatest uncertainty. Lines indicate the projected change in relative selection strength for forest cover (%), elevation (km), and distance from fresh water (km) due to changes in temperature within the species' current extent. Shaded areas indicate the mean 95% Bayesian credible intervals. Changes are relative to the relative selection strength in 2020 across the four Shared Socioeconomic Pathways (SSPs). The SSPs are listed in order of similarity to current conditions, from SSP 1-2.6 (sustainability, best-case scenario) to 5-8.5 (fossil-fueled development, worst-case scenario).

7. spatial projections of RSFs in 2020 and 2100



175

176 4 Discussion

- 177 • as temperatures get warmer, we will be pushing into the unknown portion of the surface
- 178 plots
- 179 • our models don't include any physiological responses to temperature that may impact
- 180 movement (e.g., hibernation)
- 181 • our models also assume the behaviour we modeled now will persist into the future
- 182 (e.g., hibernation, migration)
- 183 • based on the model, temperature doesn't affect grizzlies' hibernation much, and their
- 184 displacement in winter is very low due to $P(\text{moving})$ being so low:
- 185 • if the RSS decreases a lot, individuals may disperse, populations may relocate, or stay
- 186 where they are and suffer

187 **4.1 Effects of temperature on mammals' movement**

188 **4.2 Effects of temperature on mammals' habitat selection**

189 **4.3 Consequences for conservation**

- 190 • changes in temperatures are pushing to areas in the surface plots that have little
- 191 data and may be poorly estimated. We will need to extrapolate to prepare for future
- 192 changes, which implies some degree of inevitable risk. The best way to avoid this is by
- 193 designing models that are statistically sound and interpretable. The models we present
- 194 provide an estimate of the changes in behavior, but they are not tailored specifically
- 195 to any of the species in the dataset. Species-specific models should account for more
- 196 particular variables (e.g., forest age for caribou) and use dynamic resource rasters (i.e.,
- 197 not use a static estimate of forest cover). Nonetheless, we present important results for
- 198 understanding how mammals will respond to changes in climate and weather during
- 199 the next ~75 years.

- 200 • energetics
- 201 • GPS sampling intervals were large: need more work on fine-scale movement, including
- 202 accounting for multiple movement states (e.g., traveling, grazing, resting, hunting, etc.).
- 203 this would help deal with over-dispersion
- 204 • encounter rates (lower encounter rates with food (Hou *et al.*, 2020))
- 205 • HWI

²⁰⁶ **References**

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