

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

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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 air temperature data,
⁴⁵ we estimate how mammals altered their movement frequency, movement speed, and habi-
⁴⁶ tat selection in response to air temperature. We then pair the estimated responses with
⁴⁷ climate change projections to forecast changes in mammalian movement in 2100 under dif-
⁴⁸ ferent climate-change scenarios (Shared Socioeconomic Pathways, see Riahi *et al.*, 2017). We
⁴⁹ discuss the consequences of these changes in movement behavior with regards to energetics,
⁵⁰ encounter rates, habitat conservation, and human-wildlife conflicts.

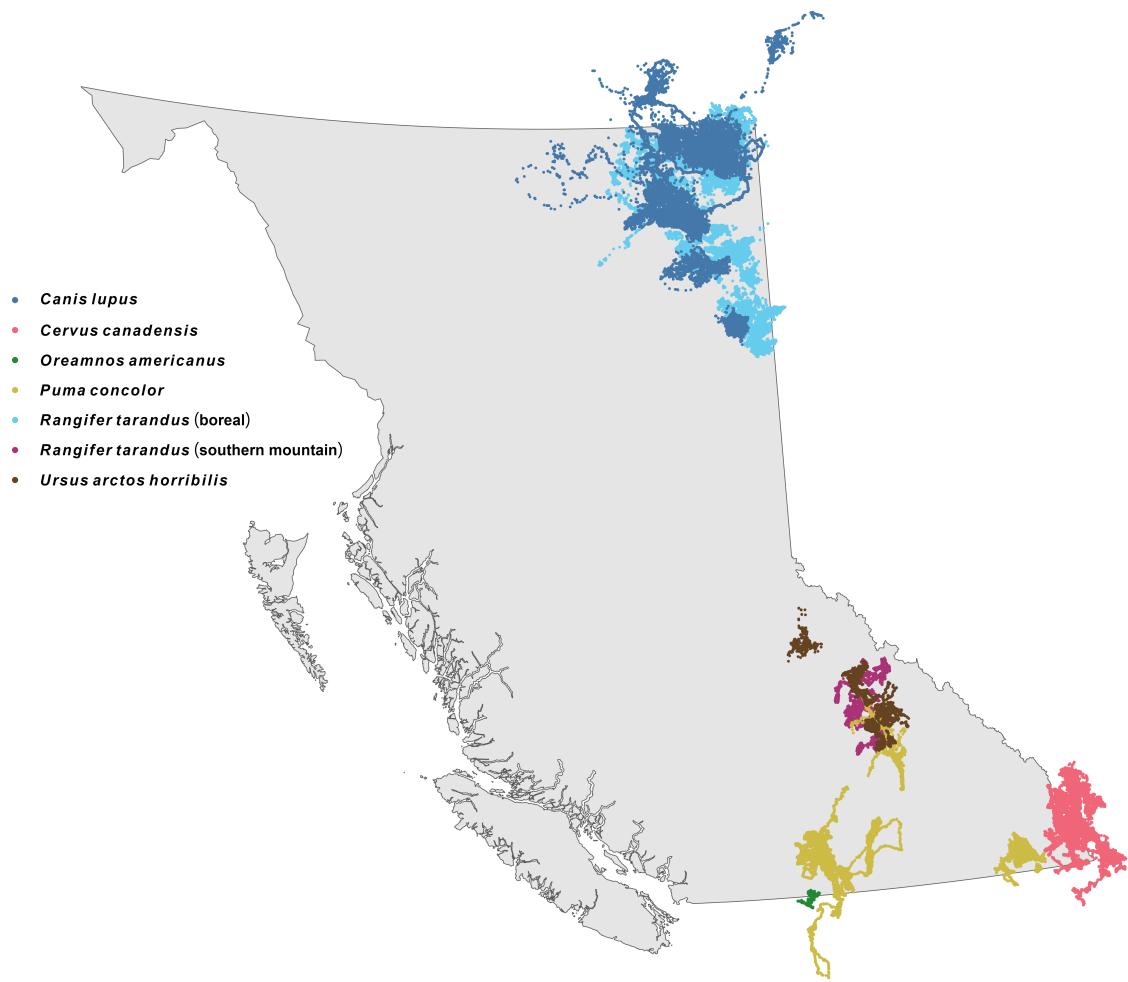


Figure 1: GPS telemetry data and 95% autocorrelated kernel density utilization distributions for the six species in this study.

Table 1: Start and end of the GPS telemetries along with the median sampling interval (Δt ; stratified by individual) and number of animals with unresolved speed (NA speed) for each of the species in this study.

Dataset	Start	End	Median Δt (hours)	NA speed
<i>Canis lupus</i>	2013-01-27	2017-08-29	0.25	0
<i>Cervus canadensis</i>	2007-01-13	2013-11-20	2.00	0
<i>Oreamnos americanus</i>	2019-06-25	2023-10-05	6.25	1
<i>Puma concolor</i>	2006-02-05	2021-07-13	2.00	0
<i>Rangifer tarandus</i> (boreal)	2011-03-02	2018-01-04	13.00	15
<i>Rangifer tarandus</i> (s. mountain)	1998-03-21	2009-06-07	6.00	2
<i>Ursus arctos horribilis</i>	2004-09-30	2009-09-07	1.00	0

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.bcgoris.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 associated custom func-
 64 tions are available on GitHub (<https://github.com/QuantitativeEcologyLab/bc-mammals->
 65 temperature).

66 **2.2 Historical temperature data**

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

73 **2.3 Estimating mammals' instantaneous speeds**

74 We modeled each animal's movement using continuous-time movement models (Fleming *et*
75 *al.*, 2014) via the `ctmm` package (version 1.2.0, Fleming & Calabrese, 2023) for `R`. We then
76 estimated mammals' instantaneous speeds by applying the `ctmm::speeds()` function on all
77 models with finite speed estimates (416 of 433, see Fleming *et al.*, 2014; Noonan *et al.*, 2019).
78 The 18 telemtries with insufficiently fine sampling were for one mountain goat, 15 boreal
79 caribou, and 2 southern mountain caribou (Table 1).

80 Since `ctmm`'s movement models assume stochastic but non-zero speeds (i.e., a single,
81 stochastic moving state), data-informed speeds needed to be corrected so that the minimum
82 instantaneous speed could be 0. We performed this correction by subtracting each model's
83 mean speed while assuming speeds were χ^2 -distributed. The function we used is avail-
84 able on GitHub at <https://github.com/QuantitativeEcologyLab/bc-mammals-temperature/>
85 `blob/main/functions/detrend_speeds.R`. To avoid artifacts due to excessively small, non-
86 zero speeds, we determined whether an animal was moving or not using the inflection point
87 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' movement state (moving or not) and
91 speed (when moving) using two Hierarchical Generalized Additive Models (HGAMs, see
92 Pedersen *et al.*, 2019 and the code chunk below) with the `mgcv` package for R (version 1.9-1,
93 Wood, 2017). The first HGAM estimated the probability that an animal was moving with a
94 binomial family of distributions and logit link function. The second HGAM estimated an an-
95 imal's speed (when moving) with a gamma family of distributions and log link function. The
96 HGAMs included random intercepts for each animal (`s(..., bs = 're')`), fixed intercepts
97 for each species, and species-level factor smooth interactions for time of day, day of year,
98 and temperature (`s(..., bs = 'fs')`, see model S in Figure 4 of Pedersen *et al.*, 2019).
99 Additionally, the models had three tensor product interaction terms (`ti()`) for each species:
100 (1) day of year and time of day, (2) temperature and time of day, and (3) temperature and
101 day of year. These three terms accounted for: (1) seasonal changes in day length, (2) hourly
102 changes in the response to temperature (e.g., changes in nocturnality), and (3) seasonal
103 changes in the response to temperature (e.g., changes in coats and migration timing). The
104 HGAMs accounted for the cyclicity of time of day and day of year using cyclic cubic splines
105 (`bs = 'cc'`, Wood, 2017). Together, the binomial HGAM and the gamma HGAM inform us
106 on an animal's long-term average speed, since it is the product of the probability the animal
107 is moving and its average speed when moving. We fit the models with fast REML ('fREML')
108 and discretized covariates (`discrete = TRUE`) to optimize computational efficiency with no
109 appreciable losses to model performance (Wood, Goude & Shaw, 2015; Wood *et al.*, 2017;
110 Li & Wood, 2020). Additional details are provided in Appendix A.

```
m_moving <- bam(  
  moving ~  
    s(animal, bs = 're') +  
    species + #' necessary since `by` terms do not include intercept terms  
    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_speed <- 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)))

```

111 2.4.2 Habitat selection

112 We estimated the effects of temperature on each species' selection for percent forest cover,
 113 elevation, and distance from fresh water (i.e., not sea water) using an HGAM with a Poisson
 114 family of distributions and log link function for each species (Appendix B, also see Aarts
 115 *et al.*, 2008; Alston *et al.*, 2022). While we recognize there are other important drivers of
 116 habitat selection that we did not include in our models (e.g., forest age), we decided to only
 117 use these three proxies to produce results that are relatively comparable between species and
 118 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)

```

Smooth effects of percent forest cover, elevation, and distance to fresh water accounted for the species-level average selection strength for each resource. A random effect for each individual animal corrected for uneven sampling across individuals, while factor smooth interaction terms (`bs = 'fs'`) accounted for individual-level resource selection (i.e., individual-level deviations from the species-level average). Finally, tensor interaction product terms (`ti()`) of the three resources and temperature estimated the change in resource selection at different temperatures. Detections were down-weighted proportionally to their degree of dependence temporally proximate detections (see Appendix C and Alston *et al.*, 2022), while quadrature points had a weight of 1.

2.5 Predicting changes in animal movement during the current century

Rasters of projected monthly average temperature in BC from 2020 to 2100 were obtained via the `climatenaR` package (version 1.0, Burnett, 2023) for R. Since the climate projections only provided monthly means and ranges but no measures of variance or distributional assumptions, we used the hourly ERA5 data for BC from 1998 to 2023 (extremes included, see

133 Hersbach *et al.*, 2023) to calculate within-month variance, which we defined as the variance
134 within a given pixel, month, and year. We then modelled the estimated variance using a GAM
135 for location and scale (GAMLS, see Rigby & Stasinopoulos, 2005; Stasinopoulos & Rigby,
136 2007). The linear predictor for the location (i.e., the mean) included smooth terms of the
137 within-pixel monthly mean temperature (for each year), month (as a cyclic smooth), a two-
138 dimensional smooth of space, and a tensor interaction product term of space and month. The
139 linear predictor for the scale term (which governs the mean-variance relationship) included
140 smooth terms of the monthly mean, month, and space. Additional details are available in
141 Appendix C.

142 We simulated for hourly variation in weather by assuming temperature followed a normal
143 distribution with mean specified by the `climatenA R` climate projections and variance as
144 specified by the Gamma GAMLS. We then predicted changes in movement behavior and
145 habitat selection as a function of temperature using the HGAMs and HRSFs along with the
146 temperature HGAM described above. For each month within each year from 2020 to 2100,
147 we simulated hourly weather by including temperatures from the 0.1, 0.2, ..., 0.8, 0.9 quantiles
148 and weighted each quantile proportionally to the (normalized) Gaussian probability density
149 for each value (Appendix C).

150 3 Results

151 3.1 Effects of temperature on movement rates

152 Partial effect of temperature varied across species (Fig. **A X**), even after accounting for
153 differences in daily and seasonal activity (e.g., sleeping, migration, hibernation; see Fig.
154 **A X**). Smooth interaction terms were well-behaved and indicated clear shifts in daily activity
155 for all species. The models explained reasonably high proportions of the deviance (11% for
156 the binomial model and 79% for the Gamma model) and had good in-sample prediction (Fig.
157 **A X**).

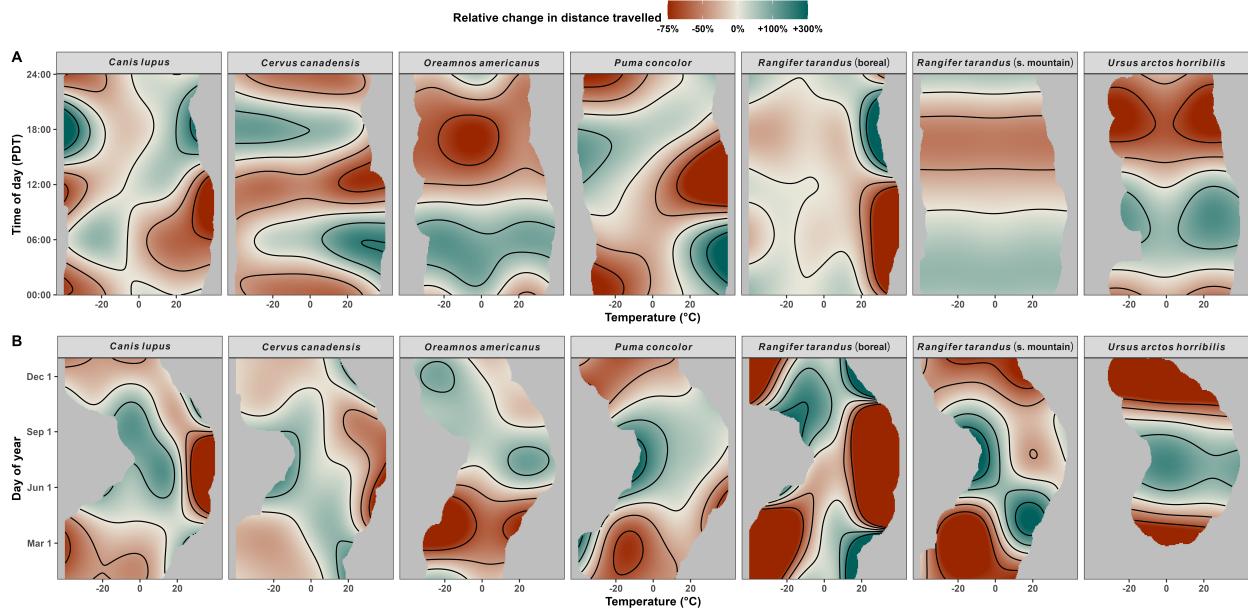


Figure 2: **Temperature is a strong determinant of how far and when mammals' travel.** Estimated effects of temperature on relative change in distance travelled (probability of moving times speed when moving) over time of day (A) and day of year (B). Predictions in the surface plots extend to 10% of 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.

158 Both movement frequency and speed when moving decreased with increasing sampling
159 interval, with a strong common effect (Fig. **A**X). *here*
160 **ctmm** models are scale independent assuming single, homogeneous behavior, but scale-
161 dependency in the behavior (data) causes sampling effects. See poor projections for boreal
162 caribou, which have the greatest sampling interval
163 worse climate-change scenarios corresponded to greater changes in behavior along with
164 greater variance in within years

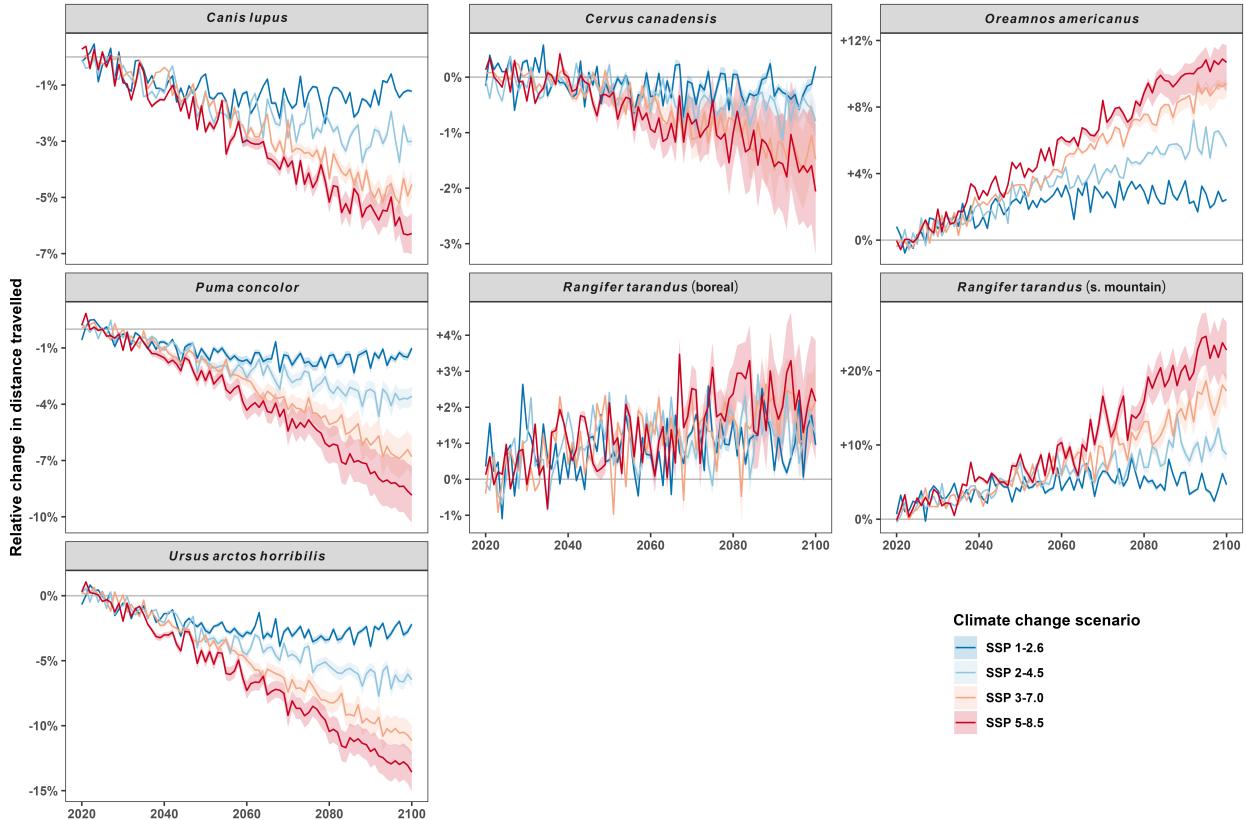
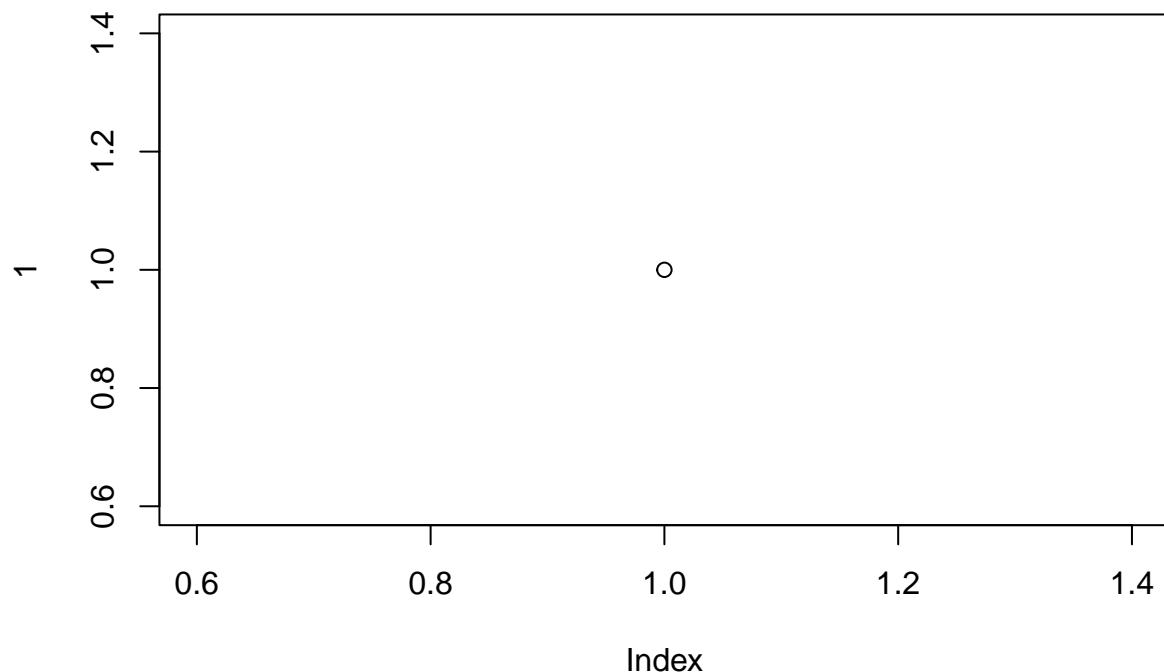


Figure 3: **The intensity and direction of changes in movement rates due to climate change vary among species, but worse climate-change scenarios consistently result in the greatest change and greatest uncertainty.** Lines indicate the projected relative change in mean distance travelled (probability 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 movement behavior (i.e., movement frequency and speed) and ignore changes in physiology or movement costs.

¹⁶⁵ 3.1.1 Predicted changes in movement during the current century

4. spatial projections of distance in 2020 and 2100



¹⁶⁶

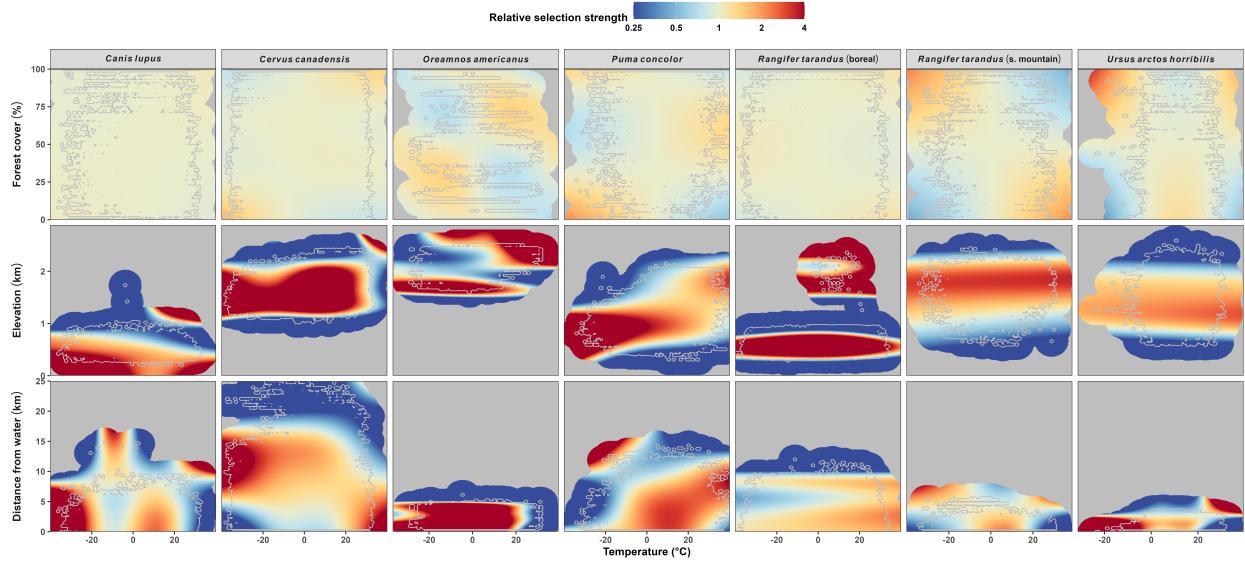


Figure 4: **Central message.** Estimated resource selection strength for forest cover (%), elevation (km), and distance from fresh water (km) as a function of temperature. The grey contours indicate the extent of each species' observed locations.

6. temporal projections of RSFs within current area

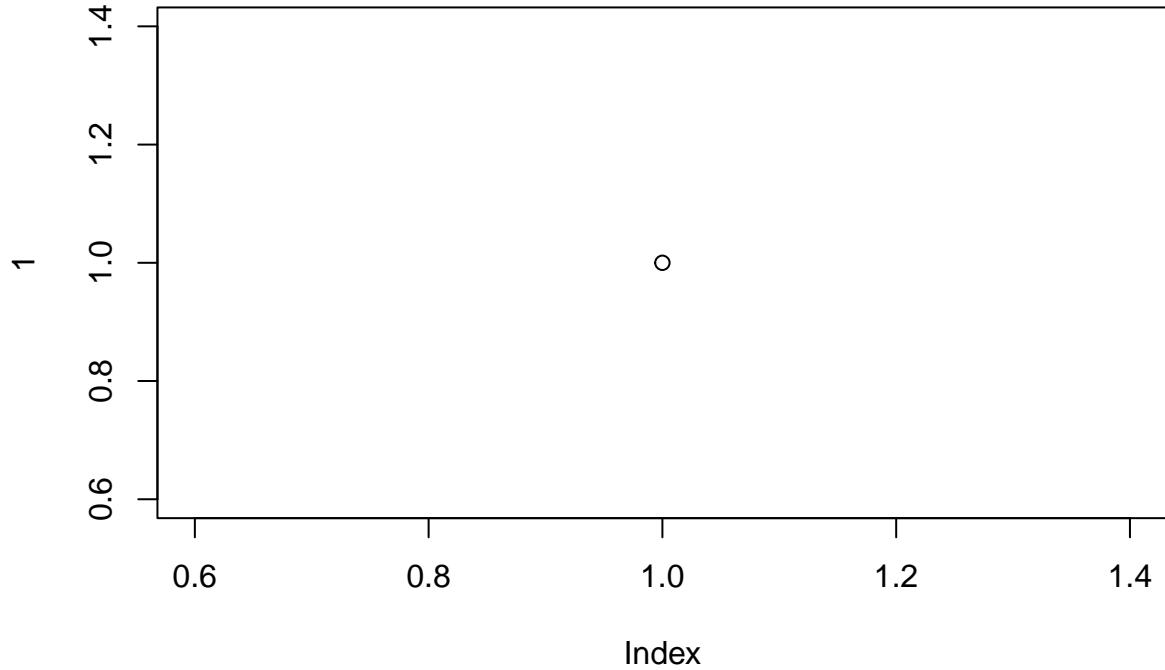
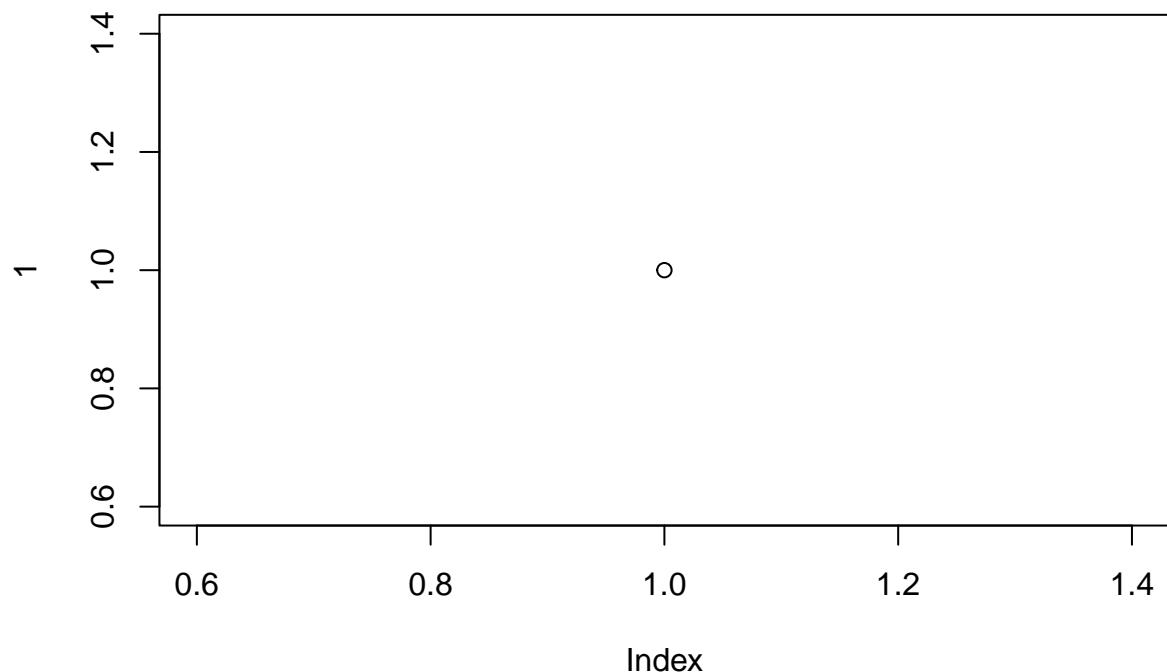


Figure 5: **The intensity and direction of changes in habitat selection vary among species, but worse climate-change scenarios consistently result in the greatest change and greatest uncertainty.** Lines indicate the projected change in relative selection strength for forest cover (%), elevation (km), 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).

¹⁶⁷ 3.2 Effects of temperature on habitat selection

¹⁶⁸ 3.2.1 Predicted changes in movement during the current century

7. spatial projections of RSFs in 2020 and 2100



¹⁶⁹

170 4 Discussion

- ¹⁷¹ We discuss the consequences of these changes in movement behavior with regards to energetics, encounter rates, habitat conservation, and human-wildlife conflicts.
- ¹⁷³ as temperatures get warmer, we will be pushing into the unknown portion of the surface plots
- ¹⁷⁵ our models don't include any physiological responses to temperature that may impact movement (e.g., hibernation)
- ¹⁷⁷ our models also assume the behaviour we modeled now will persist into the future (e.g., hibernation, migration)

- 179 • based on the model, temperature doesn't affect grizzlies' hibernation much, and their
180 displacement in winter is very low due to $P(\text{moving})$ being so low:
181 • if the RSS decreases a lot, individuals may disperse, populations may relocate, or stay
182 where they are and suffer

183 **4.1 Effects of temperature on mammals' movement**

184 **4.2 Effects of temperature on mammals' habitat selection**

185 **4.3 Consequences for conservation**

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

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

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