

Predicting how climate change will affect terrestrial mammals' movement and habitat selection

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1 Abstract

2 To do

3 Introduction

Animals’ energetic costs depend strongly on ambient temperature (Brown et al. 2004). Cold temperatures increase the metabolic costs of movement (Taylor, Heglund, and Maloiy 1982) and homeothermy (Melin et al. 2023), which can constrain an animal’s ability to move (Schwerdt, De Villalobos, and Ferretti 2024), its fitness (Walker et al. 2019), and, ultimately, its odds of survival (Berger et al. 2018). Hot temperatures tend to lower energetic needs (Taylor, Heglund, and Maloiy 1982), but they also cause animals to overheat, which lowers their ability to move (Powers et al. 2017; Alston et al. 2020; Dyer et al. 2023).

Mammals reduce the adverse effects of extreme temperatures through both physiological and behavioral adaptations (Jessen 2001; Mota-Rojas et al. 2021), but their ability to respond through physiological adaptations is limited by their evolutionary history, since their optimal temperature and range of tolerable temperatures (Fig. 1) depend on the environment they live in (Levins 1974). In contrast, changes in movement rates and space use allow mammals to respond to stressors immediately (Alston et al. 2020, 2020; Dyer et al. 2023; Attias et al. 2018; Giroux et al. 2023; Verzuh et al. 2023).

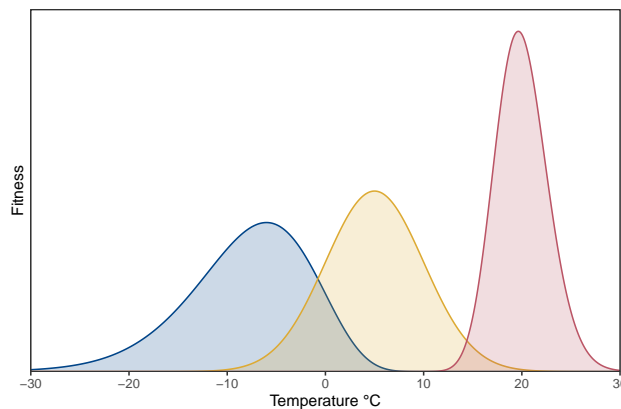


Figure 1: Hypothetical ranges in fitness as a consequence of ambient temperature for a cold-adapted mammal (blue), temperate-adapted mammal (yellow), and hot-adapted mammal (red). Contrast the differences in fitness gains at different temperatures, as well as differences in the height and spread of the three curves.

During the last century, changes in climate in British Columbia (BC), Canada, have resulted in widespread warming, milder and shorter winters, hotter and longer summers, and a greater risk of extremely high temperatures (Eberle, Higuera Roa, and Sparkes 2022).

These changes are expected continue over the next 100 years and compound their effects on mammals’ fitness, movement behavior, and habitat selection as they cope with growing heat stress and human pressure (Deb, Forbes, and MacLean 2020; Woo-Durand et al. 2020; Weststrate et al. 2024).

This paper provides a BC-focused analysis on the effects of proximate weather and long-term climate on the movement of terrestrial mammal species. Using over two decades of telemetry data and proximal hourly weather data, we estimate how animals altered their movement frequency, movement speed, and habitat selection in response to air temperature. We then pair these responses with climate change projections to forecast changes mammals movement in the current century under different climate change scenarios (Riahi et al. 2017). The analyses include data from six species (*Canis lupus*, *Cervus elaphus*, *Oreamnos americanus*, *Puma concolor*, boreal and southern mountain *Rangifer tarandus*, and *Ursus arctos horribilis*; see Table 1) across a large spatial range of British Columbia (Fig. 2). We discuss the consequences of changes in mammalian movement in relationship to energetics, food encounter rates, and the incidences of human-wildlife.

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

Dataset	Start	End	Median sampling interval (hours)
<i>Canis lupus (boreal)</i>	2013-01-27	2017-08-29	0.25
<i>Elk in southwestern Alberta</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 (boreal)</i>	2011-03-02	2018-01-04	12.99
<i>Rangifer tarandus (southern mountain)</i>	1998-03-21	2009-06-07	5.98
<i>Ursus arctos horribilis</i>	2004-09-30	2009-09-07	1.00

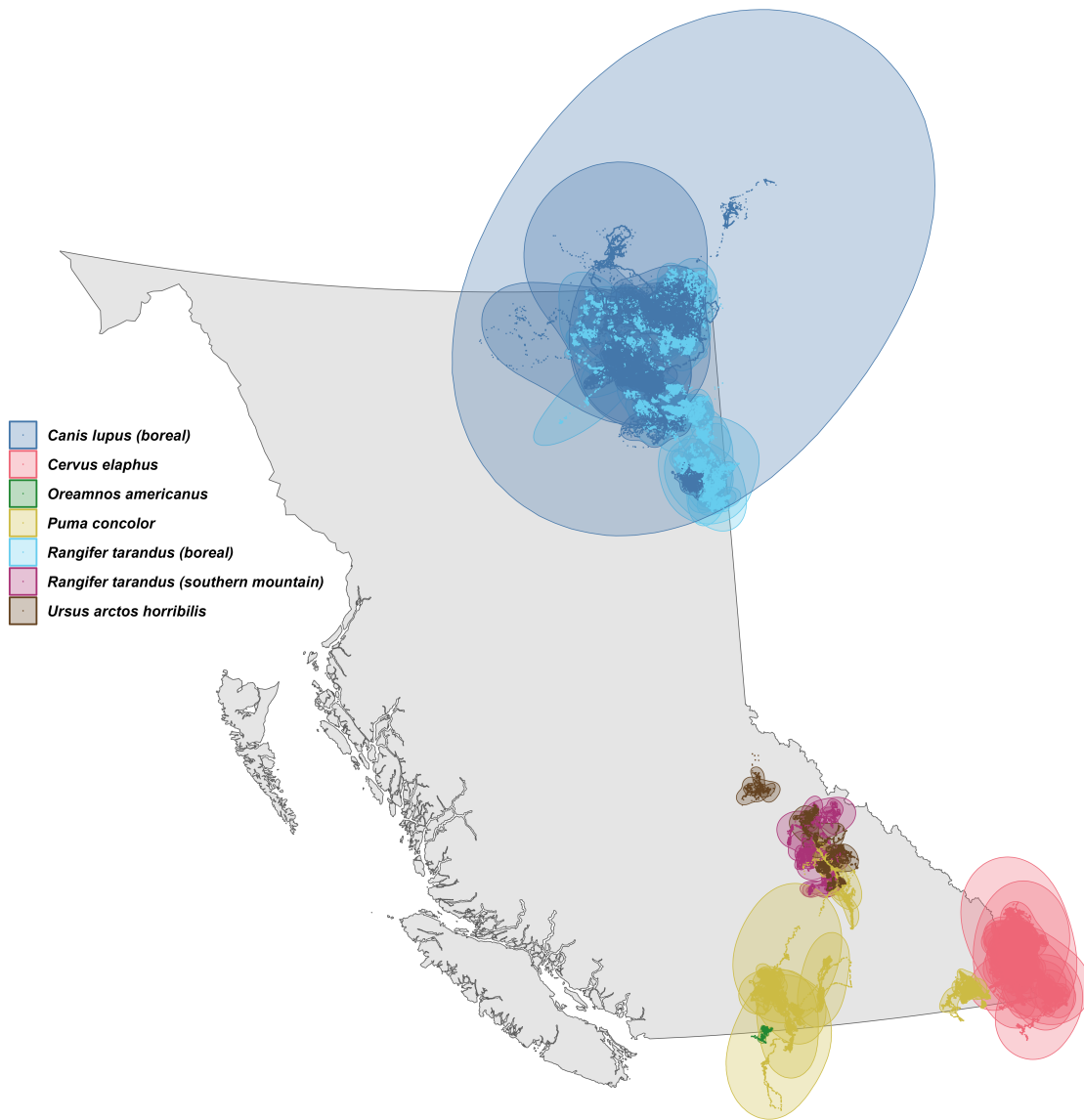


Figure 2: GPS telemetry data and autocorrelated kernel density utilization distributions for the six species included in this study.

4 Methods

4.1 Data acquisition

4.1.1 GPS telemetry data

Animal telemetry datasets were obtained from multiple sources. Elk tracking data were obtained from Movebank (Kays et al. 2022; study name: Elk in southwestern Alberta, see Ciuti et al. 2012), while the boreal caribou and wolf data were obtained from a public BC Oil and Gas Research and Innovation Society repository (<https://www.bcogris.ca/projects/boreal-caribou-telemetry-data/>). ***All other tracking data were obtained from private collaborators (refs_to_studies?).*** Outlier GPS locations were removed following diagnostic analyses of the location of each point as well as straight-line displacement and turning angle between consecutive points. Particular attention was paid to points with large turning angles ($\gtrsim 170^\circ$), especially if points before or after the potential outlier indicated stationary behavior. The script used to clean the data and all custom functions used are available on GitHub (<https://github.com/QuantitativeEcologyLab/bc-mammals-temperature>).

4.1.2 Historical temperature data

Rasters of three-hour reanalyzed air temperature data were downloaded from the ERA5 dataset (Hersbach et al. 2023) from the European Center for Medium-range Weather Forecasting server (ECMWF; www.ecmwf.int; <https://cds.climate.copernicus.eu>). Proximal weather conditions were then estimated for each location by extracting the values from the corresponding cell from the temporally nearest raster using the `extract()` function from the `terra` package for R (version 1.7-46, Hijmans 2023).

4.2 Data modeling

4.2.1 Estimating mammals' instantaneous speeds

Animal movement models were fit using the `ctmm` package (version 1.1.0, Fleming and Calabrese 2021) for R (R Core Team 2023). Mammals' speeds were then estimated using the `ctmm::speeds()` function on all models with speed estimates (Noonan et al. 2019). Most telemetries (416 of 433) had sufficiently frequent locations to provide appropriate speed estimates. All 17 telemetries with insufficiently fine sampling were for caribou (15 boreal and 2 souther mountain).

Since `ctmm`'s movement models allow for stochastic speeds but assume constant movement, speeds were set to zero if they were not significantly different from zero ($\alpha = 0.05$), under the assumption of a χ -distributed speeds. ***NOT SURE IF THIS IS CORRECT*** The function used is available on GitHub (https://github.com/QuantitativeEcologyLab/bc-mammals-temperature/blob/main/functions/detrend_speeds.R). To avoid artifacts due to excessively small, non-zero speeds, estimated speeds were then clustered into two groups using a k -means algorithm with two centers (see Appendix A).

4.2.2 Effects of temperature on mammals' movement

We estimated the effects of hourly temperature on mammals' movement using two Hierarchical Generalized Additive Models (HGAMs, see Pedersen et al. 2019) via `mgcv` package for R. The first HGAM had a binomial family of distribution and estimated the probability of a mammal moving as a function of time of day, day of year, and temperature. Since there was substantial variation in the direction and wiggleness of each species' trends, the effects were modeled independently by smooths for each species (see model I in Figure 4 of Pedersen et al. 2019). The model accounted for the cyclicity of time of day and day of year using cyclic cubic splines, which provide continuity in the smooth term by ensuring the function and its slope (first derivative) and curvature (second derivative) are continuous between con-

secutive cycles. The second HGAM had the same structure, but it used a Gamma family of distributions to estimate the speed of an animal given that it was moving. Together, the two HGAMs inform us on an animal’s long-term speed (i.e., distance traveled per unit time), since it is the product of probability that the animal is moving and the speed it moves at, given that it is moving.

4.2.3 Effects of temperature on mammals’ habitat selection

An animal’s habitat selection is proportional to the number of times one can observe it in an environment. Consequently, one can view the spatial distributions of an animal in space as a poisson process whose mean depends on the amount of space, Δu , and time, Δt , the observation takes place over, which we can write as $\lambda(\Delta u, \Delta t)$. If we shrink both Δu and Δt to a single point in space and a single moment in time, we now have $\lambda(u, t) \leq 1$, since we cannot observe more than one animal in a given point in time and space (u, t) . Additional theoretical background is provided by Aarts et al. (2008) and Alston et al. (2022) and in Appendix B.

Under the assumption of a Poisson family of distributions, we estimated the effects of temperature on each species’ habitat selection by fitting a Resource Selection Function (RSF) via an HGAM using the `mgcv` package. *here*

4.3 Predicting changes in animal movement during the current century

4.3.1 Climate change projections

Rasters of monthly average temperature in BC during the next 80 years were obtained via the `climatenR` package [version XXX; Burnett (2023)] for R. Since the climate projections of monthly average temperatures did not provide a measure of temperature variance for each month, we estimated within-month variance using a Generalized Additive Model with a Gamma family of distributions fit via the `mgcv` package for R (Wood 2017). Additional details are provided in Appendix C.

5 Results

5.0.1 Effects of temperature on mammals' movement

5.0.2 Effects of temperature on mammals' habitat selection

should predict for the area the animals are in only

6 Discussion

6.0.1 Effects of temperature on mammals' movement

6.0.2 Effects of temperature on mammals' habitat selection

- energetics
- encounter rates (lower encounter rates with food (Hou et al. 2020))
- HWI

7 References

- Aarts, Geert, Monique MacKenzie, Bernie McConnell, Mike Fedak, and Jason Matthiopoulos. 2008. “Estimating Space-Use and Habitat Preference from Wildlife Telemetry Data.” *Ecography* 31 (1): 140–60. <https://doi.org/10.1111/j.2007.0906-7590.05236.x>.
- Alston, Jesse M., Christen H. Fleming, Roland Kays, Jarryd P. Streicher, Colleen T. Downs, Tharmalingam Ramesh, Björn Reineking, and Justin M. Calabrese. 2022. “Mitigating Pseudoreplication and Bias in Resource Selection Functions with Autocorrelation-informed Weighting.” *Methods in Ecology and Evolution*, November, 2041–210X.14025. <https://doi.org/10.1111/2041-210X.14025>.
- Alston, Jesse M., Michael J. Joyce, Jerod A. Merkle, and Ron A. Moen. 2020. “Temperature Shapes Movement and Habitat Selection by a Heat-Sensitive Ungulate.” *Landscape Ecology* 35 (9): 1961–73. <https://doi.org/10.1007/s10980-020-01072-y>.
- Attias, Nina, Luiz Gustavo Rodrigues Oliveira-Santos, William F. Fagan, and Guilherme Mourão. 2018. “Effects of Air Temperature on Habitat Selection and Activity Patterns of Two Tropical Imperfect Homeotherms.” *Animal Behaviour* 140 (June): 129–40. <https://doi.org/10.1016/j.anbehav.2018.04.011>.
- Berger, J., C. Hartway, A. Gruzdev, and M. Johnson. 2018. “Climate Degradation and Extreme Icing Events Constrain Life in Cold-Adapted Mammals.” *Scientific Reports* 8 (1): 1156. <https://doi.org/10.1038/s41598-018-19416-9>.
- Brown, James H., James F. Gilgooly, Andrew P. Allen, Van M. Savage, and Geoffrey B. West. 2004. “Toward a Metabolic Theory of Ecology.” *Ecology* 85 (7): 1771–89. <https://doi.org/10.1890/03-9000>.
- Burnett, Michael. 2023. *climatenaR: Tools to Access ClimateNA Data*.
- Ciuti, Simone, Tyler B. Muhly, Dale G. Paton, Allan D. McDevitt, Marco Musiani, and Mark S. Boyce. 2012. “Human Selection of Elk Behavioural Traits in a Landscape of Fear.” *Proceedings of the Royal Society B: Biological Sciences* 279 (1746): 4407–16.

<https://doi.org/10.1098/rspb.2012.1483>.

- Deb, Jiban Chandra, Graham Forbes, and David A. MacLean. 2020. “Modelling the Spatial Distribution of Selected North American Woodland Mammals Under Future Climate Scenarios.” *Mammal Review* 50 (4): 440–52. <https://doi.org/10.1111/mam.12210>.
- Dyer, Alexander, Ulrich Brose, Emilio Berti, Benjamin Rosenbaum, and Myriam R. Hirt. 2023. “The Travel Speeds of Large Animals Are Limited by Their Heat-Dissipation Capacities.” Edited by Anders Hedenström. *PLOS Biology* 21 (4): e3001820. <https://doi.org/10.1371/journal.pbio.3001820>.
- Eberle, Caitlyn, Oscar Higuera Roa, and Edward Sparkes. 2022. “Technical Report: British Columbia Heatwave.” United Nations University - Institute for Environment; Human Security (UNU-EHS). <https://doi.org/10.53324/GZUQ8513>.
- Fleming, Christen H., and Justin M. Calabrese. 2021. *Ctmm: Continuous-Time Movement Modeling*. <https://CRAN.R-project.org/package=ctmm>.
- Giroux, Aline, Zaida Ortega, Nina Attias, Arnaud Léonard Jean Desbiez, Denis Valle, Luca Börger, and Luiz Gustavo Rodrigues Oliveira-Santos. 2023. “Activity Modulation and Selection for Forests Help Giant Anteaters to Cope with Temperature Changes.” *Animal Behaviour* 201 (July): 191–209. <https://doi.org/10.1016/j.anbehav.2023.04.008>.
- Hersbach, H, B Bell, P Berrisford, G Biavati, A Horányi, J Muñoz Sabater, J Nicolas, et al. 2023. “ERA5 Hourly Data on Single Levels from 1940 to Present.” Copernicus Climate Change Service (C3S) Climate Data Store (CDS). <https://doi.org/10.24381/CDS.ADBB2D47>.
- Hijmans, Robert J. 2023. *Terra: Spatial Data Analysis*. <https://CRAN.R-project.org/package=terra>.
- Hou, Rong, Colin A. Chapman, Ollie Jay, Songtao Guo, Baoguo Li, and David Raubenheimer. 2020. “Cold and Hungry: Combined Effects of Low Temperature and Resource Scarcity on an Edge-of-range Temperate Primate, the Golden Snub-nose Monkey.” *Ecography* 43 (11): 1672–82. <https://doi.org/10.1111/ecog.05295>.

- Jessen, Claus. 2001. *Temperature Regulation in Humans and Other Mammals*. Berlin, Heidelberg: Springer Berlin Heidelberg.
- Kays, Roland, Sarah C. Davidson, Matthias Berger, Gil Bohrer, Wolfgang Fiedler, Andrea Flack, Julian Hirt, et al. 2022. “The Movebank System for Studying Global Animal Movement and Demography.” *Methods in Ecology and Evolution* 13 (2): 419–31. <https://doi.org/10.1111/2041-210X.13767>.
- Levins, Richard A. 1974. *Evolution in Changing Environments: Some Theoretical Explorations*. 3. printing. Monographs in Population Biology 2. Princeton, NJ: Princeton Univ. Press.
- Melin, M., J. Matala, L. Mehtätalo, J. Pusenius, and T. Packalen. 2023. “The Effect of Snow Depth on Movement Rates of GPS-Collared Moose.” *European Journal of Wildlife Research* 69 (2): 21. <https://doi.org/10.1007/s10344-023-01650-w>.
- Mota-Rojas, Daniel, Cristiane Gonçalves Titto, Agustín Orihuela, Julio Martínez-Burnes, Jocelyn Gómez-Prado, Fabiola Torres-Bernal, Karla Flores-Padilla, Verónica Carvajal-de La Fuente, and Dehua Wang. 2021. “Physiological and Behavioral Mechanisms of Thermoregulation in Mammals.” *Animals* 11 (6): 1733. <https://doi.org/10.3390/ani11061733>.
- Noonan, Michael J., Christen H. Fleming, Thomas S. Akre, Jonathan Drescher-Lehman, Eliezer Gurarie, Autumn-Lynn Harrison, Roland Kays, and Justin M. Calabrese. 2019. “Scale-Insensitive Estimation of Speed and Distance Traveled from Animal Tracking Data.” *Movement Ecology* 7 (1): 35. <https://doi.org/10.1186/s40462-019-0177-1>.
- Pedersen, Eric J., David L. Miller, Gavin L. Simpson, and Noam Ross. 2019. “Hierarchical Generalized Additive Models in Ecology: An Introduction with Mgecv.” *PeerJ* 7 (May): e6876. <https://doi.org/10.7717/peerj.6876>.
- Powers, Donald R., Kathleen M. Langland, Susan M. Wethington, Sean D. Powers, Catherine H. Graham, and Bret W. Tobalske. 2017. “Hovering in the Heat: Effects of Environmental Temperature on Heat Regulation in Foraging Hummingbirds.” *Royal Society Open Science* 4 (12): 171056. <https://doi.org/10.1098/rsos.171056>.

- R Core Team. 2023. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Riahi, Keywan, Detlef P. van Vuuren, Elmar Kriegler, Jae Edmonds, Brian C. O'Neill, Shinichiro Fujimori, Nico Bauer, et al. 2017. "The Shared Socioeconomic Pathways and Their Energy, Land Use, and Greenhouse Gas Emissions Implications: An Overview." *Global Environmental Change* 42 (January): 153–68. <https://doi.org/10.1016/j.gloenvcha.2016.05.009>.
- Schwerdt, Leonela, Ana Elena De Villalobos, and Nelson Ferretti. 2024. "Ecological Niche Modelling and Thermal Parameters to Assess the Prevalence of an Endemic Tarantula: The Endurance of *Grammostola Vachoni Schiapelli & Gerschman, 1961*." *Journal of Insect Conservation*, May. <https://doi.org/10.1007/s10841-024-00595-y>.
- Taylor, C. R., N. C. Heglund, and G. M. O. Maloiy. 1982. "Energetics and Mechanics of Terrestrial Locomotion. I. Metabolic Energy Consumption as a Function of Speed and Body Size in Birds and Mammals." *Journal of Experimental Biology* 97 (1): 1–21. <https://doi.org/10.1242/jeb.97.1.1>.
- Verzuh, Tana L., Savannah A. Rogers, Paul D. Mathewson, Alex May, Warren P. Porter, Corey Class, Lee Knox, et al. 2023. "Behavioural Responses of a Large, Heat-sensitive Mammal to Climatic Variation at Multiple Spatial Scales." *Journal of Animal Ecology* 92 (3): 619–34. <https://doi.org/10.1111/1365-2656.13873>.
- Walker, William H., Olga Hecmarie Meléndez-Fernández, Randy J. Nelson, and Russel J. Reiter. 2019. "Global Climate Change and Invariable Photoperiods: A Mismatch That Jeopardizes Animal Fitness." *Ecology and Evolution* 9 (17): 10044–54. <https://doi.org/10.1002/ece3.5537>.
- Weststrate, Dayna K., Aimee Chhen, Stefano Mezzini, Kirk Safford, and Michael J. Noonan. 2024. "How Climate Change and Population Growth Will Shape Attendance and Human-Wildlife Interactions at British Columbia Parks." *Journal of Sustainable Tourism*, March, 1–15. <https://doi.org/10.1080/09669582.2024.2331228>.

- Wood, Simon N. 2017. *Generalized Additive Models: An Introduction with r*. Second edition. Chapman & Hall/CRC Texts in Statistical Science. Boca Raton: CRC Press/Taylor & Francis Group.
- Woo-Durand, Catherine, Jean-Michel Matte, Grace Cuddihy, Chloe L. McGourdji, Oscar Venter, and James W. A. Grant. 2020. “Increasing Importance of Climate Change and Other Threats to at-Risk Species in Canada.” *Environmental Reviews* 28 (4): 449–56. <https://doi.org/10.1139/er-2020-0032>.