

LINKING ENVIRONMENTAL STOCHASTICITY WITH ANIMAL SPACE USE USING
CONTINUOUS-TIME STOCHASTIC PROCESSES

by

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Abstract

Lay Summary

Preface

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Acknowledgements

Dedication

To the Lands that have nourished me and given me a place to live, learn, and play.

1 Introduction

The effects of resource abundance on animals' spatial needs have been studied by many in the last century. Multiple general hypotheses have been postulated based on (relatively) small-scale empirical studies (e.g., Burt, 1943; Southwood, 1977; Lindstedt & Boyce, 1985; Grant, 1993), and supported (or questioned) by recent work with larger, higher-resolution datasets (Jonzén *et al.*, 2006; Wolkovich *et al.*, 2012; Falcón-Cortés *et al.*, 2021; Dickie *et al.* in press) and simulations (Blackwell, 2007). Improvements of animal tracking equipment and decreases in the cost such equipment, together with growing willingness (and requirements) to share data openly (ref?; but see Roche *et al.*, 2015) have greatly increased the amount of movement data which can be modeled at once.

The increase in movement data availability allows researchers to produce more powerful results, but the high-frequency sampling often results in non-independence between temporally consecutive data. Additionally, high-frequency data is more likely to be sampled at irregular intervals. Thus, most commonly-used home range estimation methods (e.g., minimum convex polygon) cannot be used with such datasets because they assume data points to be approximately independent and at regular time intervals. While one could coarsen data to larger, regular intervals at the expense of data frequency, this nullifies great part of the benefits achieved with recent improvements in tracking technologies. Thus, it is increasingly more important to model animal movement data using models that (1) do not assume data is regularly sampled, and (2) account for the spatio-temporal autocorrelation within the data. Continuous-time models such as Ornstein-Uhlenbeck (OU) and OU foraging (OUF) models relax the assumption of spatio-temporal independence by accounting for positional autocorrelation (OU and OUF models) and directional (i.e., velocity) autocorrelation (OUF models only). Additional information on modeling is given in the modeling chapter (section 4.3.1).

continue here

- animals who have their needs met in a given area minimize their movement to avoid wasting energy. movement to a new area is often caused by inferior resource availability
- “the area traversed by the individual in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered.” (Burt, 1943)

1.1 Resource abundance

Animals' needs vary greatly between taxonomic groups, but some needs are essential for most species for survival and reproduction, such as include energetic needs (e.g., food, water), habitat needs (e.g., dens,

trees, tall grass, breeding grounds, protection from predators and competitors). Home range (HR) size is hypothesized to be proportional to resource abundance, such that HR size increases when resources are low, but the relationship is likely not monotonic nor linear, since larger home ranges can result in higher rates of competition and are harder to defend (Grant, 1993). HR size is also affected by resource (or patch) connectivity, since well-connected habitats can decrease the energetic cost of movement and increase resource exploitation rates (Dickie *et al.* in press).

... While the effects of resource abundance on HR size have been studied extensively, the effects of environmental stochasticity, including the stochasticity of resource abundance, have not been given as much consideration.

1.2 Environmental stochasticity

Environmental stochasticity has been of interest to biologists for multiple decades (e.g., Bell *et al.*, 1993), but until recently changes in variance have been hard to quantify because they require large amounts of data to produce reasonably precise and accurate estimates, especially if the variance is allowed to vary over time or space. However, the recent increase in high-frequency ecological data allows us to estimate trends in environmental stochasticity with reasonable levels of precision. In addition, advances in accessible high-level modeling software (Wood, 2017; e.g., R Core Team, 2021) and computing power allow researchers to perform sophisticated analyses using (relatively) accessible and inexpensive equipment.

The recent shift to more quantitative statistical methods in environmental biology has pushed people to begin thinking more critically about data analysis, ... The question of how much data is needed to detect a significant trend (**how-much-data-for-significant-trend?**) may seem important to some, but I suggest we pay less attention to whether an event or trend is statistically significant over a period of time based on an arbitrary dichotomy (e.g., $p < \alpha = 0.05$). Since statistical significance does not only depend on effect size but also sample size (including measurement frequency), high-frequency data is likely to produce statistically significant effects, even in the event of a false positive. Instead, we should focus primarily on whether a change has an important impact on the fitness of the animal(s) of interest.

What an animal perceives as a stochastic process depends on the stochasticity of the process relative to the animal's size and current age (or average lifespan). Small-scale processes will have greater effects on smaller animals than on bigger ones: the grazing pattern of a bison (*Bison bison*) drastically alters the habitat of most crawling insects, but other grazing mammals would not pay attention to changes in grass length at the same spatial resolution. Similarly, the yearly snowfall would be a predictable and expected event for most

adult moose (*Alces alces*), but it may be a shock for many adult zooplankton or a new-born wolf (*Canis lupus*). Thus, what may be perceived as a series of highly variable and unpredictable events by one animal may be considered as a single stochastic event by another, while a third may even see the change as part of a larger, long-term, predictable process (figure 1). Whether the increase in resource availability in figure 1a is considered as part of a larger process (dark blue line), a single increase (orange line), or three separate increases (light blue line) does not only depend on the timescale of the event(s) but also the perceived timescale of the event(s), which depends greatly on the age, lifespan, and memory of the animal observing the event. Generally, small, short-lived, or young organisms will tend to be more sensitive to small-scale or short-term changes (Southwood, 1977).

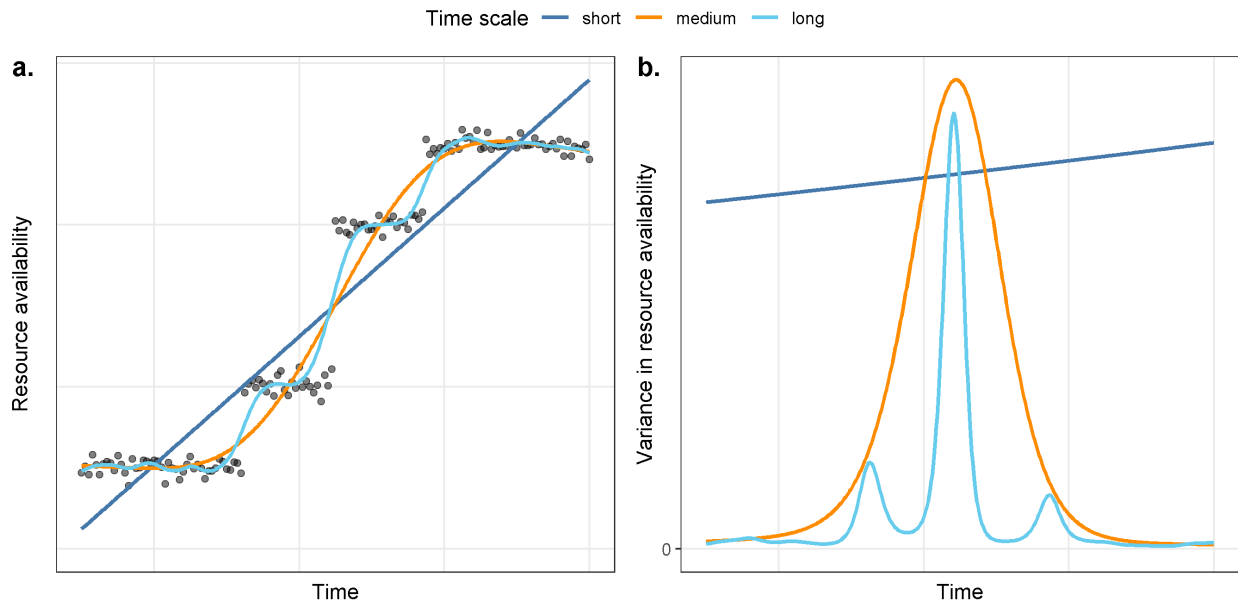


Figure 1: Hypothetical perceptions of changes in fictitious resource abundance. Events which occur over very short time periods (e.g., $< 0.01\%$ of an animal's life) may be perceived as a single event or part of a larger event, and the animal may not perceive small-scale changes. If the event occurs over a longer (but still short) period (e.g., $< 10\%$ of an animal's life), the change may be perceived as a separate event with a smooth increase in mean resource availability and a single peak in variance. Finally, the event occurs during the majority of the organism's life, the increases in mean resource availability would likely be perceived as three separate events, with four different plateaus and three distinct peaks in variance.

Figure 1 could also be interpreted based on *perceived* time scale rather than the true duration of an event, although the two measures are somewhat related. In this case, animals which perceive events as occurring over a short (i.e., negligible) time scale would likely perceive the increase in resource abundance as a single change, whether this occurs over a short period of time or not. In contrast, animals which perceive the process as three separate increases may have a fairly different view of the process. If the same process is perceived as occurring over three different time scales, animals may develop different levels of adaptability

and memory relative to it. Animals which perceive the process as a single event would likely show a small, monotonic change in behavior or not react at all. In contrast, animals which perceive the process as one or multiple changes may react one or more times and may be more likely to remember the change as one or more distinct and important events. *not sure about this section, but I thought I'd write it anyway*

Tie to *The time scale of stochastic events*

Different types of environmental stochasticity:

- spatial stochasticity:
 - environmental patches and niches,
 - habitat heterogeneity
- temporal stochasticity:
 - events (heat domes, fires, tornadoes, storms)
 - events are hard to predict when:
 - * they do not occur frequently within an organism's generation time
 - * they occur frequently but unpredictably common but stochastic (i.e., $p \approx 0.5$)
- spatio-temporal stochasticity (in the inclusive sense, not just the interaction):
 - alternate stable states
 - ephemeral habitats following stochastic events (e.g. burned forest, flooded area – but compare to yearly flooded areas such as temperate forests)

Small-scale patch structure in North American and South: * Alone, fire homogenizes while herbivory diversifies, but together they diversify the most (Fuhlendorf and Engle 2004; Archibald et al. 2005; Collins and Smith 2006)

notes:

- <https://www.greensensefarms.com/home>
- <https://onlinelibrary.wiley.com/doi/10.1111/plb.12085>
- https://spinoff.nasa.gov/Spinoff2018/cg_7.html
- predictable events: lizard's alternating gate to minimize contact time on hot sand
- The γ -variance between spatiotemporal points at a given (spatiotemporal, multidimensional) lag \vec{h} is calculated as

$$\gamma(\vec{h}) = \frac{1}{2} \mathbb{E} \left[Z(\vec{x} + \vec{h}) - Z(\vec{x}) \right]^2 = \frac{1}{2} \text{Var} \left[Z(\vec{x} + \vec{h}) - Z(\vec{x}) \right]$$

(Bachmaier & Backes, 2011). The $\frac{1}{2}$ is because we don't need to repeat each pair (e.g., $V((a, b), (b, a)) =$

$2V((a, b))$. View $\gamma(\vec{h})$ as a function of \vec{h} rather than a fixed value.

1.2.1 The time scale of stochastic events

When quantifying stochastic events, the severity and frequency of the events should be scaled relative to an organism’s generation time (**ref?**). Events which are stochastic but occur frequently will lead an organism to develop protective mechanisms, particularly if such events pose a high risk of mortality or injury. *How do animals from areas with frequent extreme events (e.g., sand storms) avoid damage? Do they use dens or develop a resistance?* Bison (*Bison bison*) have fur to protect them from cold winds, and they stand in groups facing the wind to decrease heat loss and damage from the cold.

As the occurrence of an event become more unpredictable (i.e., less common), the effect of such events may be very destructive in the moment, but recovery may be possible. In contrast, if the magnitude of an event and its damage become more stochastic, recovery may be harder to achieve. As extreme events become more frequent, the variance in occurrence increases until the events become common. For a Bernoulli random variable with probability of occurrence p , $Y \sim Ber(p)$, the variance (i.e., stochasticity) is maximized when $p = 0.5$ and lowest when the event occurs almost never ($p \approx 0$) or almost always ($p \approx 1$).

As a extreme events becomes more common, organisms may begin to adapt to their occurrence, as long as the change in frequency is sufficiently gradual to allow adaptation.

If stochastic events become common, animals may learn to “store for a rainy day.” For instance, if the probability of a downpour at night in a desert is high but highly unpredictable ($p \approx 0.5$), animals and plants may develop protective mechanisms [e.g. cacti closing their flowers at sunset; Stanton *et al.* (2010)]. When extreme events occur frequently, . If a dangerous event becomes more frequent and unpredictable, organisms may tend to take advantage of favorable times so they can resist more adverse times. Frequent destructive events may be less dangerous than infrequent destructive events. Events which do not occur frequently during an organism’s generation time or lifespan (e.g., 2 times or less) may not be considered as threats worth preparing for. In contrast, stochastic and destructive events which happen frequently become part of an organism’s habitat, and such organisms may adapt to their occurrence and even learn to predict them (**ref?**).

The time to re-colonization of a habitat (also see the *rescue effect* sensu **ref?**) will not necessarily be proportional to the organisms’ generation times. The movement of organisms with short generation times tends to be shorter because generation time correlates with mass (**ref?**). Thus, organisms with short generation times (e.g., aquatic invertebrates, see Kolasa, Hewitt & Drake, 1998) are more likely to move slowly or be

moved by large and potentially unpredictable events (e.g., waves, tides, sea currents, storms).

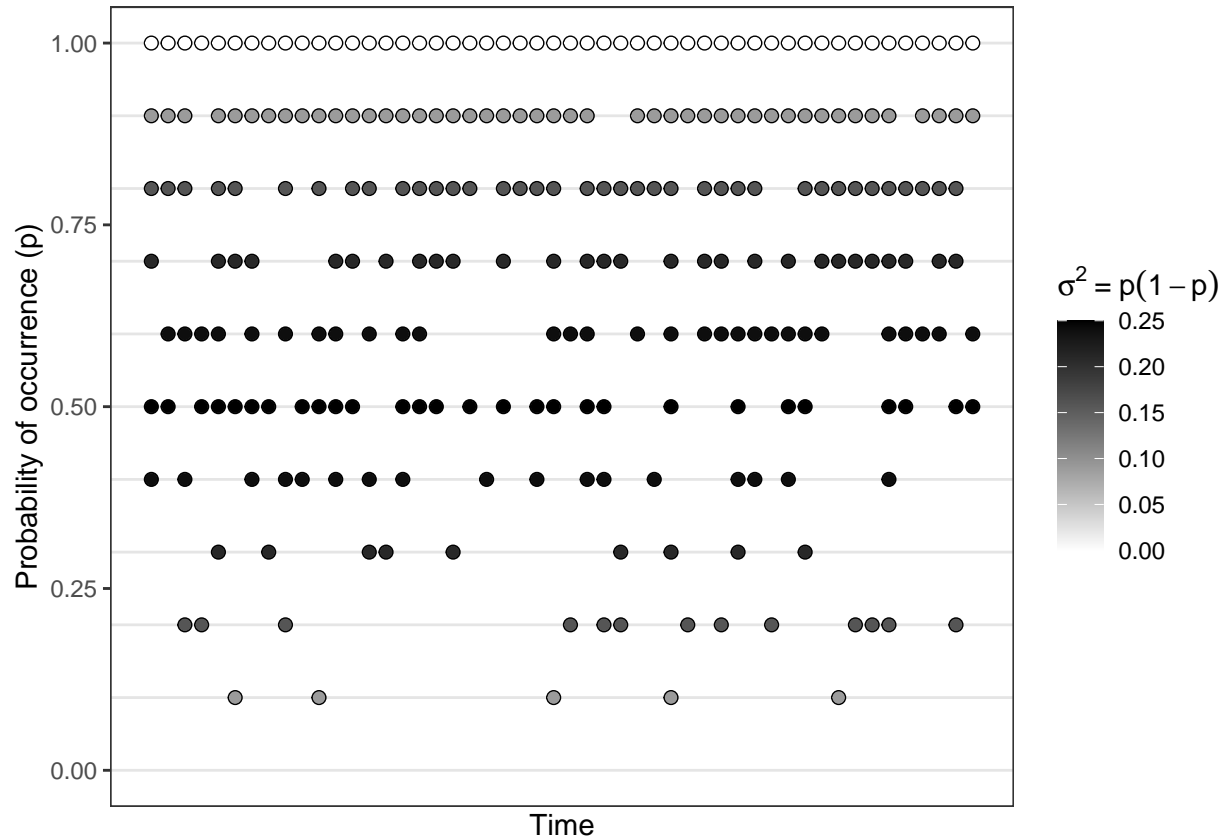


Figure 2: Realizations of Bernoulli processes for different probability parameters, p . At low values of p , successes occur unpredictably

In the case of obligate symbiosis or interaction, a species' ability to change its range or adapt will likely depend strongly on its associate's ability to move or adapt, too.

Large-scale studies such as this one are useful to detect general and common trends, while small scale studies such as the work of Kolasa *et al.* (1998) can provide more information on the small-scale drivers of phenomena.

An animal's ability to alter its behavior and movement in response to environmental conditions is essential in stochastic or changing landscapes. Whether the changes be due to highly variable but (potentially) predictable changes such as climate change and the weather, or whether they be due to more stochastic events (e.g., fires, floods, oil spills), an animal's ability to adapt increases its odds of survival. Rickbeil *et al.* (2019) showed that the yearly migration of elk (*Cervus canadensis*) depends on variable environmental events and cues such as available forage biomass, hunting pressure, snow fall, and snow melt. Birds have also shown to change their their migration as the climate changes, including trans-Saharan migrants (Jonzén *et*

al., 2006).

An organism's dependence on stochastic cycles such as changes in temperature, precipitation, and resource availability is more efficient and more plastic than depending on purely deterministic cycles (e.g., photoperiod). While this thesis focuses on the movement and spatial use of animals, the adaptability (or lack thereof) of non-animal organisms is also crucial. The ability of most animals to rely on visual cues and move accordingly greatly increases their adaptability and plasticity, particularly for those animals that are able to move large distances over short periods of time (e.g., birds, large vertebrates). Since plants and fungi cannot rely on visual cues nor move as easily, they must depend more on effective reproduction timing, seed dispersal, and evolution of the species rather than the fitness of the individual (**ref?**). Recent changes in flowering and leafing times of plants have been estimated, but changes are occurring faster than predicted by experimental estimates by as much as 4.0-8.5 times (Wolkovich *et al.*, 2012). This discrepancy between experimental and observational estimates indicates the importance of interpreting experimental results carefully and conditionally on the model and data. The underestimation suggests experimental models fail to account for important factors, such as changes in wind disturbance and soil moisture, shifts in genotypes, and community structure, as well as loss of species diversity (**ref?** on the change in phenology with species loss).

See *The effects of phenological mismatches on demography*.

Rickbeil *et al.* (2019):

- Many species use seasonal migration to track emerging resources (Fryxell, Greever, & Sinclair, 1988), reduce predation risk (Hebblewhite & Merrill, 2009), or avoid disease and parasites (Altizer, Bartel, & Han, 2011).
- Migrations to track resources are often timed to coincide with peak plant and insect emergence (Aikens *et al.*, 2017; Jonzén *et al.*, 2006; Merkle *et al.*, 2016)
- there is growing evidence that some [bird] populations are adjusting their behavior, suggesting that migration, specifically migration timing, may be more plastic than previously expected (Jonzén, Hedenstrom, & Lundberg, 2007; Jonzén *et al.*, 2006; Lameris *et al.*, 2018) and highlighting a potential measure of resilience in the face of climate change
- Elk depart earlier from highly-productive areas? This goes against the idea that animals move as a consequence of need. This could be a spurious correlation or maybe a correlation to an unaccounted effect?
- Elk left early when exposed to hunting more

1.3 Objectives

This project aims to quantify how animal’s movement and use of space are affected by the abundance of resources (e.g., food, water, breeding grounds) and environmental stochasticity. I will produce a global raster of a new environmental stochasticity index, and new quantitative methods for animal movement. Findings will inform design of protected areas and assist in conserving Canada’s wildlife, particularly in light of Canada’s pledge to protect 30% of its landmass and oceans by 2030 (Ryan Patrick Jones, 2021), although only 13% of Canada’s area is currently protected (Government of Canada, 2021). Local Indigenous groups will be included in the research process, in the hope of forming long-lasting co-operative relationships.

I will use simulation studies and an unprecedented and conservation-relevant animal tracking dataset (>1500 animals, 77 globally-distributed species) to provide the most detailed investigation into how animal spatial needs change with environmental stochasticity to date. This work has four key objectives: (i) estimating individuals’ spatial requirements in a way which is insensitive to variation in sampling protocols and data quality; (ii) quantifying environmental stochasticity and its effects; (iii) estimating between-species trends using models that are robust to commonly-found issues (e.g., correlations within species); and (iv) understanding how Traditional Indigenous Knowledge can be integrated into large-scale ecological research and conservation planning within a framework that acknowledges both Traditional Indigenous Knowledge and Western science (Kutz & Tomaselli, 2019).

To achieve these aims: (i) I will use continuous-time models (Johnson *et al.*, 2008) that do not depend on sampling frequency. Such models will allow me to use the entirety of the data rather than aggregated data (e.g., daily averages), as aggregated data contain less information on sample variance and can lead to biased estimates. (ii) I will produce a global, time-varying raster of environmental stochasticity which accounts for productivity (Nilsen, Herfindal & Linnell, 2005), weather, and climate (e.g., precipitation and temperature), as well as the frequency of extreme events (e.g., heat domes, flooding, forest fires). I will then use the raster to estimate the effect of stochasticity on home range sizes. (iii) I will use a hierarchical approach (Pedersen *et al.*, 2019) to estimate common trends and variances within and between populations, species, and data collection methods. (iv) I will collaborate closely with various Indigenous groups and include any Traditional Knowledge and practices they wish to include in my project. The research will be published in open-access journals and all code will be publicly available.

2 Chapter 1: Literature review with theoretical and empirical movement models

NOTES:

- make predictions/hypotheses for project
- what influences stochasticity: what is it and what is affecting it
- very little testing has been done on effects of stochasticity
- write paragraph(s) on energetics
- don't use tau for generation times because it's used for autocorrelation parameters
- linear features can facilitate movement (e.g., pipelines, seismic lines, low-traffic roads, [dickie_resource_2022?](#)) but also increase mortality (Mike's anteater study)

2.1 Resource availability and productivity

Grant (1993): - protective/defensive adaptations peaks at intermediate levels of competitor density/spatial resource density/spatiotemporal clumping. At low competition, there's no need for defense and the cost (e.g., energetic) and risk (e.g., wounds) outweigh the benefit, while at high values the cost and risk become too high and they outweigh the benefit. -

Environmental productivity is tightly linked to the amount of space that animals need to cover to obtain the resources they needed to survive and reproduce (Lucherini & Lovari, 1996; Relyea, Lawrence & Demarais, 2000). While resource availability is often considered in conservation decision-making, an environment's heterogeneity, stochasticity, and how the two change over time are rarely accounted for. In addition, environmental stochasticity, including extreme events, can reduce a landscape's energetic balance (Chevin, Lande & Mace, 2010), which, in turn, would decrease animals' fitness. Therefore, we expect animals living in unpredictable environments to require more space than those in stable environments (Fig. 1). Although this hypothesis is supported by a few recent studies (Morellet *et al.*, 2013; Nandintsetseg *et al.*, 2019; Riotte-Lambert & Matthiopoulos, 2020), many of them are limited in their analytical depth and geographic and taxonomic scales, so there remains a need for developing a more complete understanding of how animals' spatial needs change with environmental stochasticity. These stresses are compounded by climate change, which exposes species to increasingly common stochastic events (IPCC, 2018). Furthermore, anthropogenic structures reduce the habitat available to terrestrial species (Wilson *et al.*, 2016), who struggle to move in

fragmented(Fahrig, 2007), human-dominated landscapes(Tucker *et al.*, 2018). As the impacts of habitat loss and climate change will worsen in the future(Hansen *et al.*, 2013; IPCC, 2018), it is imperative that we better understand spatial requirements of taxa to protect wildlife existence and biodiversity. Environmental safeguarding is also essential for Reconciliation with Indigenous People in Canada (Truth and Reconciliation Commission of Canada, 2015).

2.2 Environmental stochasticity

If an individual is centered on prime habitat, there's only so far it can go out before it hits the bounds of its current ecosystem. Of course, the scale over which this occurs is likely to be massive, but even with infinite plasticity, there's an upper limit on how large a species range can be. But then moving to the edge can be important in patchy environments.

Let E indicate the energy an animal can access through food in a given visit to a patch or encounter with prey. Next, let V indicate the number of patch visits or prey encounters necessary for the animal to reach its energetic needs for a given time period. Let $\mathbb{E}(\cdot)$ indicate the expected (i.e., mean) of a random variable and $\mathbb{V}(\cdot)$ its variance (e.g., $\mathbb{E}(E)$ and $\mathbb{V}(E)$ for the energetic need's mean and variance, respectively).

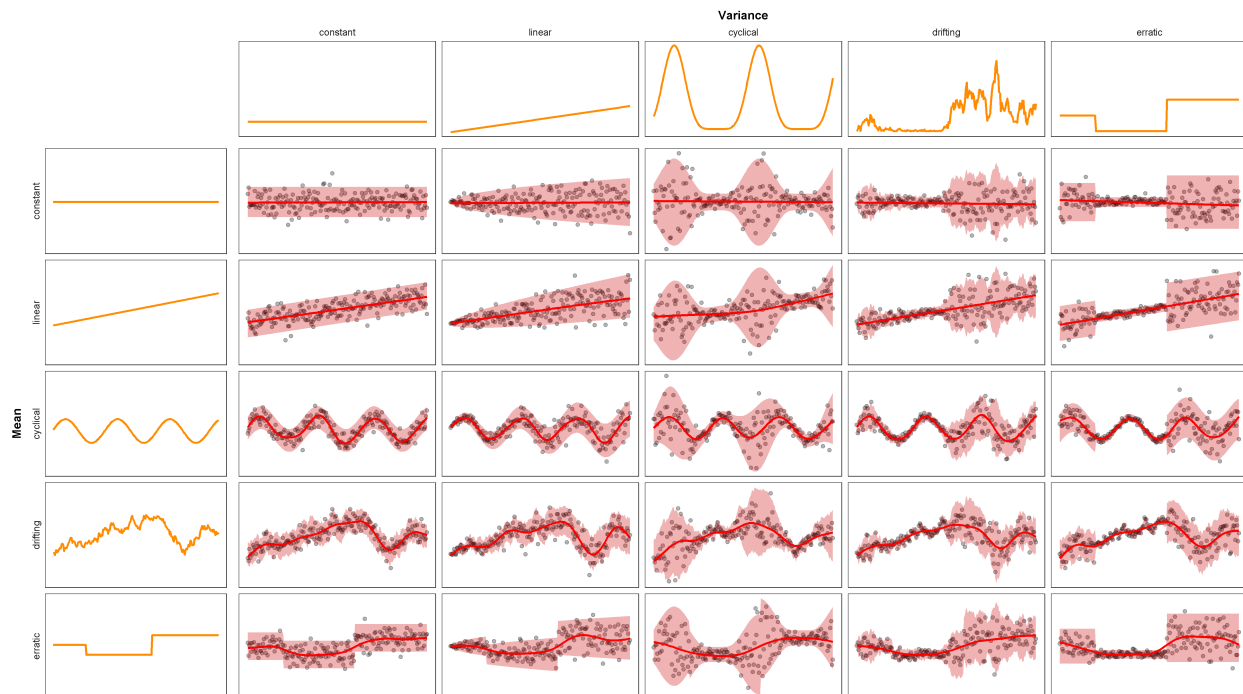


Figure 3: Simulated data with constant, linearly increasing, cyclical, drifting, and erratic means and variances. The red lines are the means estimated by a Generalized Additive Model fit by `ggplot2::geom_smooth()`, while the shaded areas are the range of ± 2 true (i.e., not estimated) standard deviations around the estimated mean.

The `geom_smooth()` shows that the amount of detail in our estimates depends directly on our data resolution (which is why some red lines don't look similar to the orange mean ones, especially for the stochastic mean). This also adds a new consideration, because the change in the mean is not the same as the variance in the data, but we cannot distinguish the two (easily).

FIX FIGURE REFERENCE IN FIGURE CAPTIONS FOR 5-5-sims AND 5-5-cv

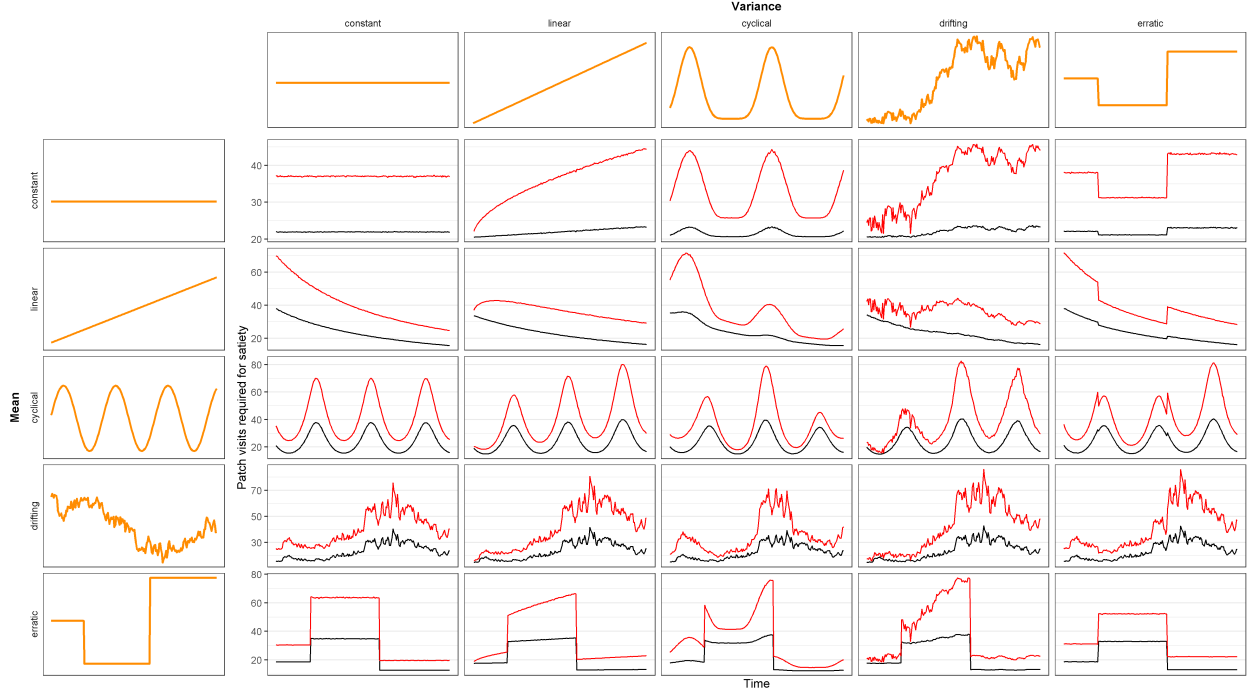


Figure 4: Simulated spatial requirements for animals living in habitats detailed in Figure ref(fig:5-5-panel). The black line indicates the mean spatial requirement needed for survival, while the red line indicates the mean requirement + 2 standard deviations. The latter can be interpreted as the minimum requirements needed for an approximate 95% chance of survival, which would be proportional to the animals' 95% home range.

Changes in variance have greater effects in highly predictable areas because changing variance from near 0 to any number is multiplicatively much larger than increasing an already large variance.

$HR = a\mathbb{E}(\text{productivity}) + bV(\text{productivity}) - c\mathbb{E}(\text{metabolic rate}) - d\mathbb{E}(\text{energetic cost of movement})$ where a, b, c, d are (estimated) coefficients.

Also, a highly stochastic variance will be estimated as a smoothly-changing variance unless we have very high amounts of data.

Apply mean VS variance 5x5 figure to HR size or location:

- there are conditions where remaining in a particular habitat becomes unsustainable and migrations or

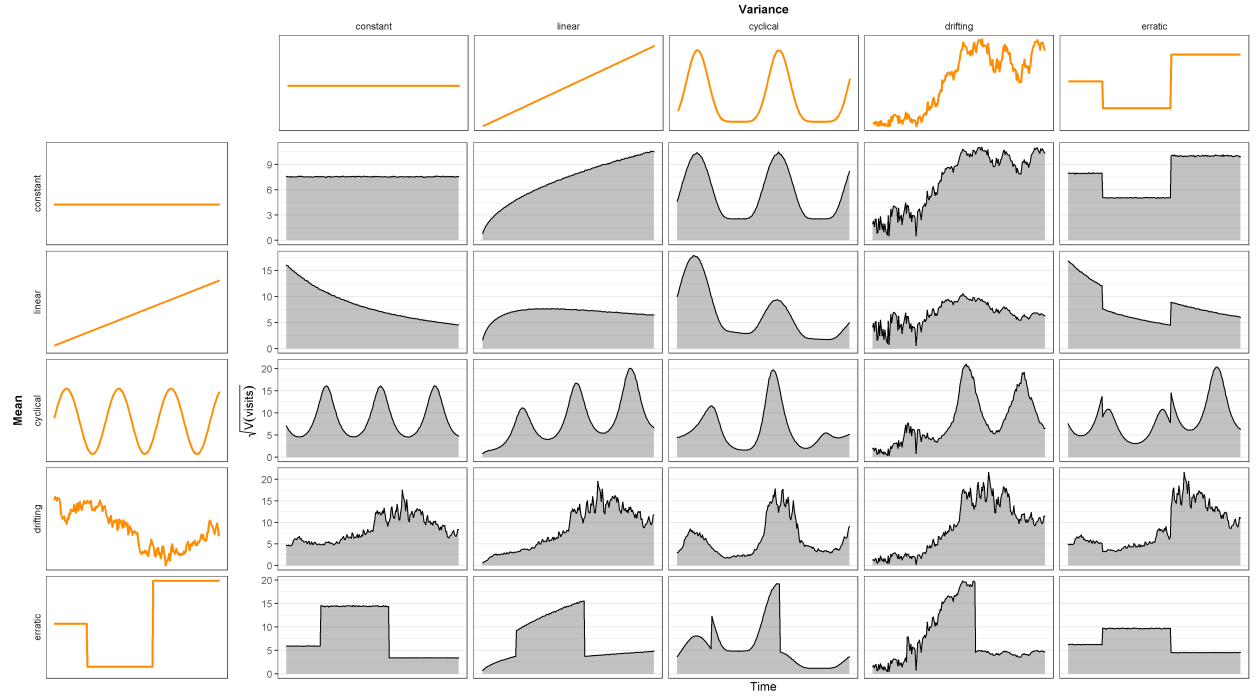


Figure 5: Standard deviations of the number of patch visits needed for an animal to survive in the habitats detailed in Figure 3. Each patch has mean resources as indicated on the left column and variances as indicated in the top row. Note that although the variance in available energy, $V(E)$, is related to the variance in patch visits, the two are not the same. More variable habitats will result in larger spatial requirements, but the relationship is not linear, since habitats with higher mean available energy result in lower spatial requirements. Additionally, the mean available energy and the .

range shifts are required for survival,

- **cyclical mean** ==> repeated migration (or diurnal cycles)
- **cyclical variance** could be because of seasonal/daily cycles in resources, temperature, precipitation
- **drifting** could be because of a highly complex ecosystem with many unpredictable agents (e.g., tropical areas with high density of insects)
- **erratic** could be because of sudden events (e.g., fires, human activity)

2.2.1 Temporal stochasticity

How an organism responds to a stochastic event broadly depends on a variety of correlated factors, including the organism's size, ability to move, lifespan, and generation time (**ref?**). Smaller organisms (e.g., mice) are more likely to be severely impacted by a stochastic event than larger ones (e.g. elephants), since larger organisms can have bigger energy reserves, can move longer distances over short periods of time, and tend to have longer lifespans, generation times, and developmental periods, which allow them to develop or memory about the frequency and severity of such events (**elephants-and-droughts-ref?**). However, the short generation time and high fertility of smaller *r-limited* species (**ref?**) can allow them to develop traits that increase the chances of survival following an extreme event. For instance, while most large trees are able to survive small-scale fires (and some even depend on them, as in the case of *pinus with serotinous cones*), many grasses survive fires by keeping most of their biomass below ground, where it is unaffected by most superficial fires.

See figures in *Southwood 1977*

Southwood 1977: - *durational stability* of a habitat (period favorable for reproduction and survival): $H = F + L$; number of generations per period: H/τ - in stable environments (i.e., with low to no stochasticity), $H \gg \tau \implies$ organisms perceive $H \rightarrow \infty$ - greater survival of the residents may simply derive from their knowledge of the geography of the habitat with the corresponding advantages for feeding and predator avoidance, noticed in animals ranging from Heliconius butterflies (Gilbert 1975; Cook, Thomason & Young 1976) to primates (MacKinnon 1974). - Cope's law? (Southwood et al. 1974, see Southwood 1977) - animals living in an area with high temporal stochasticity should exhibit more polymorphism to be able to adapt to unpredictable habitats (Southwood 1977). In areas where temporal stochasticity has or will increase as a result of climate change, we expect species will need to adopt new behaviors or become more polymorphic to survive.

Organisms are most affected by stochastic events and processes which occur on time scales which are in the order of the organisms' life spans or generation times (**ref?**). Weekly heavy rains which alter a lake's salinity

(ref?) are more likely to affect an individual than a multi-centennial drought, and the high salinity that follows the drought may be perceived as the (stressful) standard by individuals which were born during the drought. In contrast, organisms can adapt to unpredictable heavy rains if they occur on a daily frequency. However, stochastic processes and events which occur on time scales that are longer than an organism's lifespan may still cause significant effects on a population's fitness and stability. Droughts which occur on the time scale of centuries or millennia (Haig *et al.* (2013)) are unlikely to affect organisms directly, but such events could still alter the population's habitat or breeding grounds enough to cause a population collapse or prevent individuals from reproducing in their habitual breeding region (or reproduce altogether).

For an event or process to be recognized as deterministic by an individual, it must occur multiple times during the individual's lifetime (but the converse is not true). *some animals can develop memory* (Foley, Pettolelli & Foley, 2008)

Trees that have drought resilience have higher mortality (DeSoto *et al.*, 2020) *check the stats & causation from this reference*

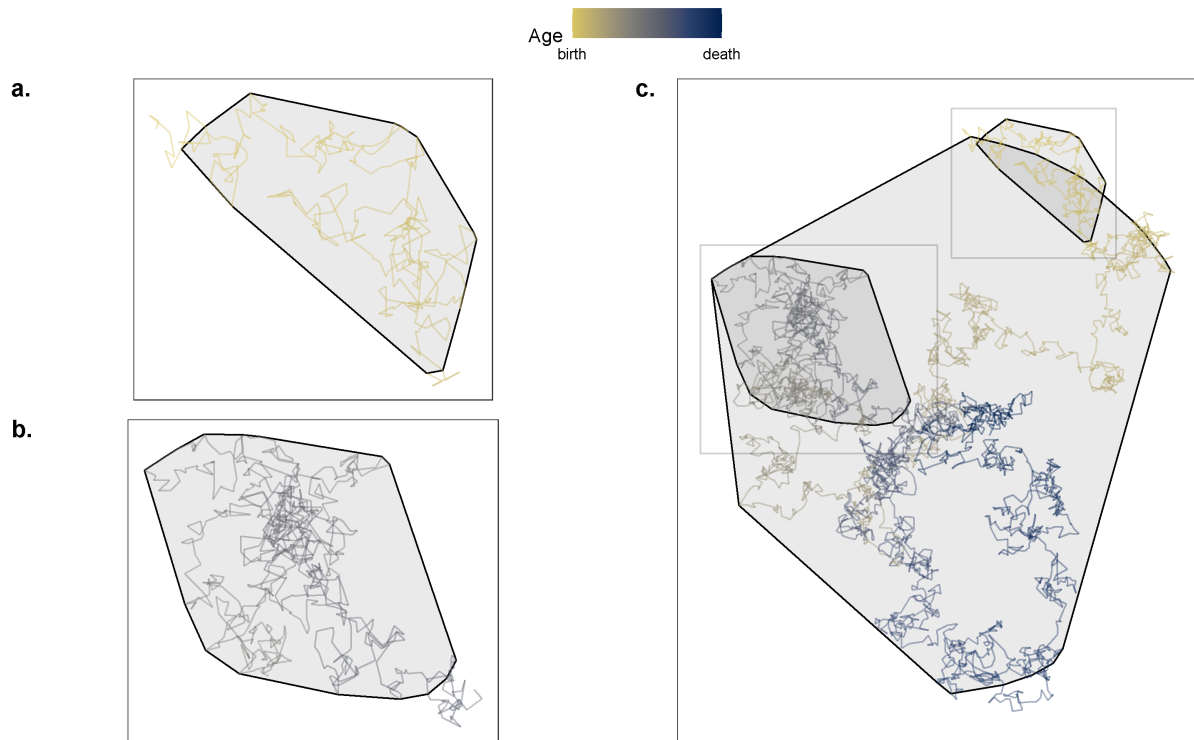


Figure 6: Simulated movement of an individual over their life. Samples from different periods of the animal's life may result in different conclusions, such as slow nomadism (a) or range residency (b), but neither sample is representative of the space the animal used over its entire life (c).

The length of an animal's lifespan and the scale of their space use can determine how we classify their

movement. However, we should minimize the bias which may arise from considering an animal's spatio-temporal scale relative to our view of time and space. If the animal tracked in figure 6 is an insect with a lifespan of one day that lives in our office, we may consider the insect range-resident relative to a space we are familiar with (the office), but if the animal is a vertebrate living in a forest, we may be more likely to consider the animal a nomad.

Distinguish between temporary spatial needs (e.g., yearly) vs long-term spatial needs (e.g., life-long). If the animal moves because of fires or human activity, we wouldn't consider it nomadic, and we should account for the full range of space, rather than the space used in a fraction of its life (e.g., panels (a) or (b)). Looking at the group it lives in may also help understand if the changes are random or not, since the entire group moving would suggest it's not random.

2.2.2 Spatial stochasticity

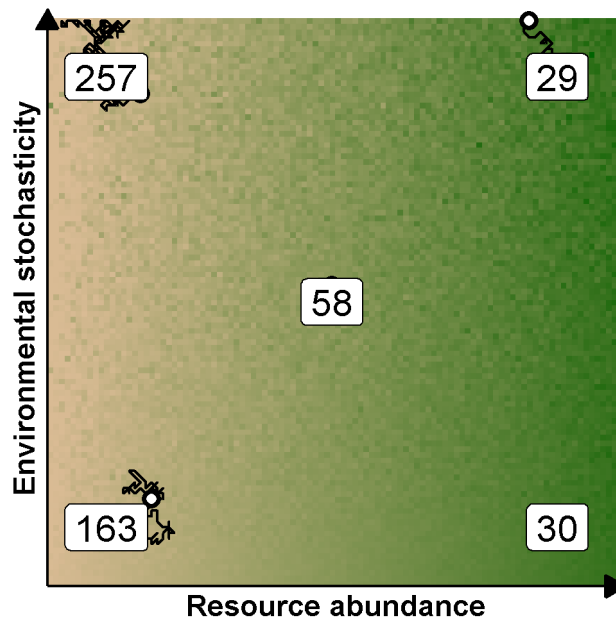


Figure 7: Simulations depicting the effects of resource availability and stochasticity on spatial needs. Animals moved from the circles to nearby tiles until satiated. The labels indicate how many steps animals took to reach satiety. Note the higher spatial needs of animals in more unpredictable or resource-scarce environments.

To measure the spatial stochasticity of an ecosystem, it is necessary to first define extent of the ecosystem of interest. A lake may seem like a simple and self-contained space to define, but it is often not as simple as deciding the lake's boundaries using a map or satellite pictures. Should one include the shores of the lake? And if so, which region do we consider the lake's shores? Are they the area of land which are currently covered by water, including the sections hit daily by waves, or should we also include the parts of land which

are currently not wet but are covered during seasons with more rain? One could base their definition on the species of interest, since coastal areas are not frequented by large fish, but they would likely include them in the ecosystem if they are studying benthic littoral species. Thus, how one measures stochasticity should also depend on which organisms are of most interest. The repetitive and cyclical motion of waves may not concern most vertebrates that live along the coast, but it is much more turbulent and chaotic for smaller organisms, such as crustaceans or diatoms. Therefore, the scale at which we consider spatial stochasticity should depend on the size of the organisms of interest as well as the size of their habitat or home range.

Bell *et al.* (1993):

- Believe “environmental variance increases indefinitely with distance or over time, so that *environments can be regarded neither as ~uniform at small spatial scales nor as random at large spatial scales~*“???
- Regions with high spatial (or spatio-temporal) variance can result in offspring experiencing conditions very different from those their parents experienced
- The scale at which we consider spatio-temporal variance is important. Bell *et al.* (1993) were unable to find a maximum value of spatio-temporal stochasticity as the distance between locations increased from the order of meters to that of hundreds of kilometers.
- Spatially autocorrelated and temporally homogeneous landscapes favor sedentary specialists, spatially independent and temporally homogeneous areas favor nomadic specialists, temporally heterogeneous favor generalist or plastic species.
- Variation can occur on multiple axes (light, food, temperature, water availability, etc.), so there can be different types of adaptations and plasticity, some of which can be more advantageous.
- Spatial variation will favor movement and behavioral adaptations faster than temporal variation will. Species in a heterogeneous landscape can move to more favorable locations, but it is harder to adapt to an unpredictable or highly variable environment.
- temporal variation should promote plasticity over diversity
- Although Bell *et al.* (1993) couldn't find a scale at which variance stopped increasing, it seems reasonable to assume that variance cannot increase infinitely. The variance of a finite system (e.g., a lake or a well-defined habitat), should reach a finite maximum somewhere between our smallest scale of interest and the scale of the entire system, even if the maximum is reached when the entire system is considered. This does not imply that a somewhat larger system that contains the first one (e.g. the lake and its coasts) will have the same variance. Variance between lake and coast is high because they are different types of habitats, and the area where they meet (the coast) is potentially even more variable

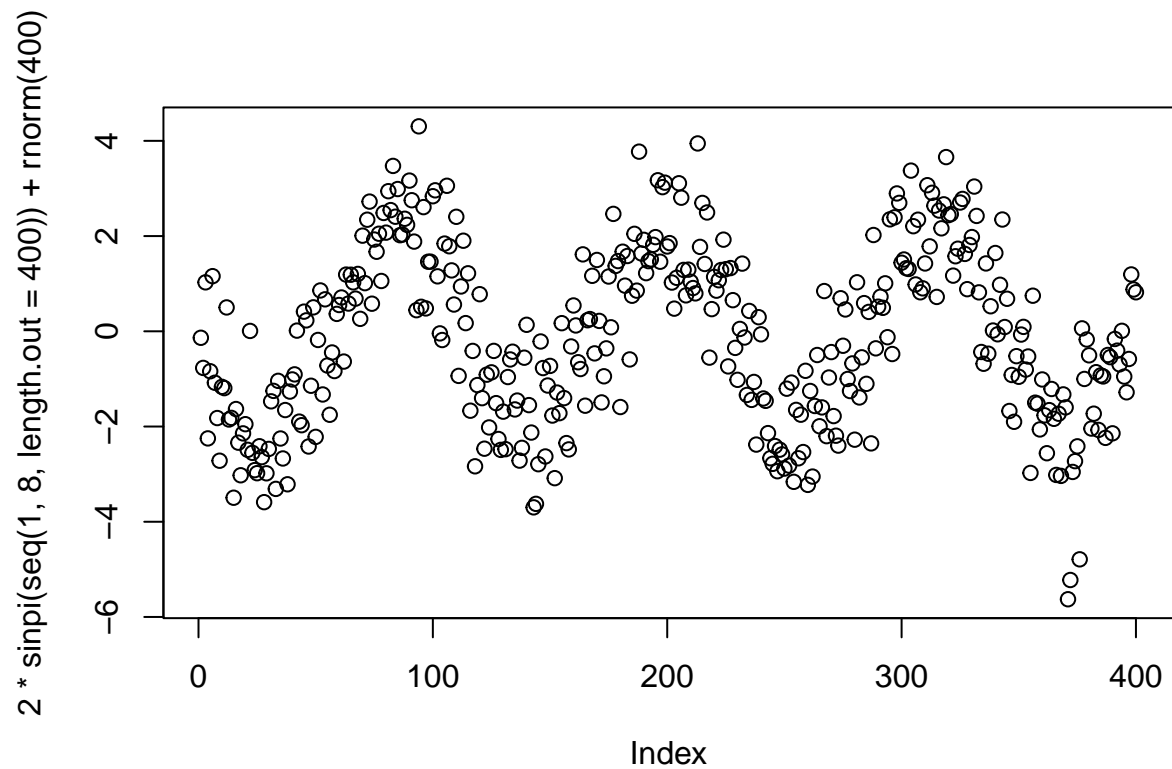
because the mixture of the two creates a third habitat for litoral benthic animals which is subject to high stochasticity due to waves and changing water levels.

non sequitur

The same idea (*that variance is finite if we consider the entire ecosystem*) would likely also apply for larger-scale systems, such as continents or a planet. And while stochasticity of a system may also vary over time, it is not reasonable to expect it to increase monotonically through time because that would imply it has been increasing monotonically until the current moment. Still, stochasticity does vary over time, and its estimation depends on the data available, so it may be useful to view it as a random variable with an estimated, conditional posterior distribution through a Bayesian framework (Bolstad & Curran, 2017). * Bell *et al.* (1993) state that they expect environmental variables to vary more than population sizes or fitness. While this may make sense conceptually, quantitatively it depends on the units used. Movement measured in miles will differ less than movement measured in meters, so comparing the two variances to the variance in resources (e.g., food, precipitation) may be futile.

Note that highly variable \neq unpredictable. E.g.: temperature change within each year can be highly variable (-40 to +40), but it is still predictable:

```
plot(2 * sinpi(seq(1, 8, length.out = 400)) + rnorm(400))
```

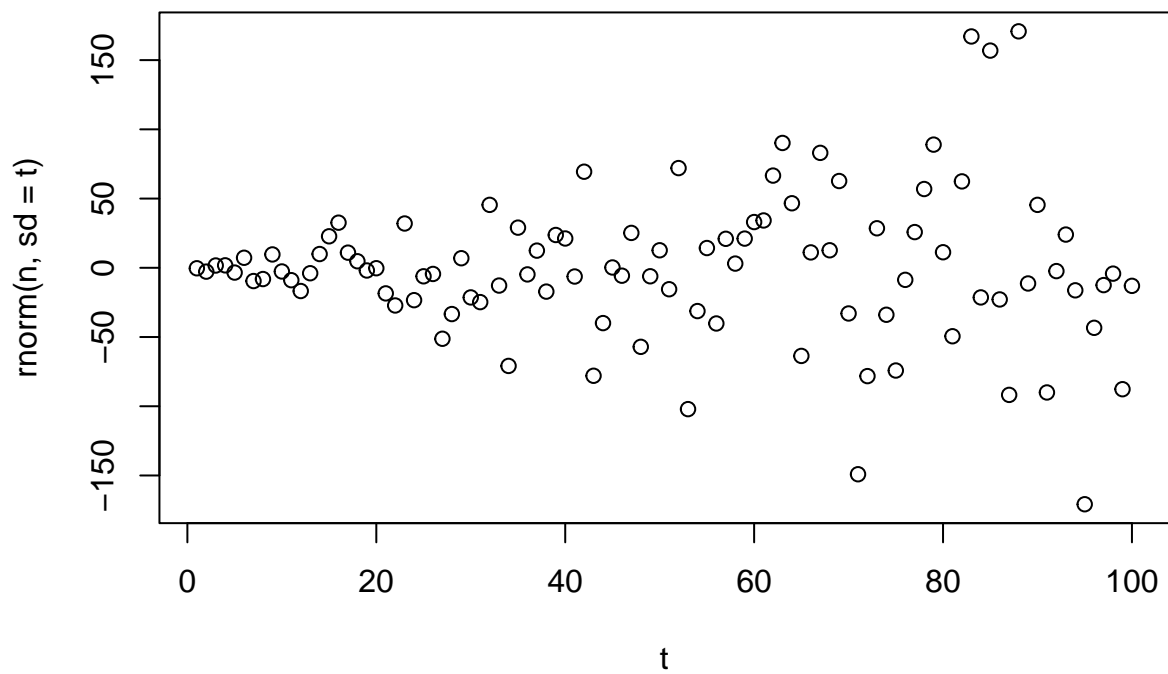


For organisms to evolve, some need to survive. If habitats are so unpredictable that most individuals cannot survive a stochastic event (whether it be as short as a fire or as long as a centennial drought), then species will not be able to evolve and adapt.

```
library('tibble')
library('tidyr')
library('ggplot2')
theme_set(theme_bw())

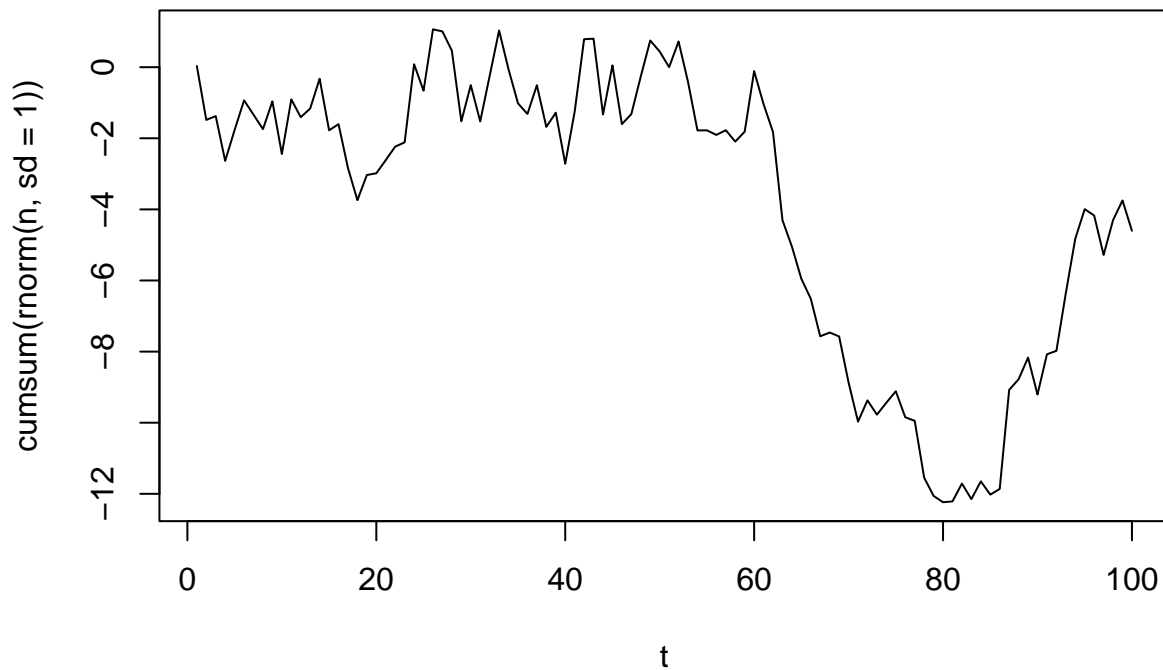
n <- 100
t <- 1:n

# instantaneous variance increases over time
plot(t, rnorm(n, sd = t))
```



variance between time points t and $t-k$ increases over time

```
plot(t, cumsum(rnorm(n, sd = 1)), type = 'l')
```

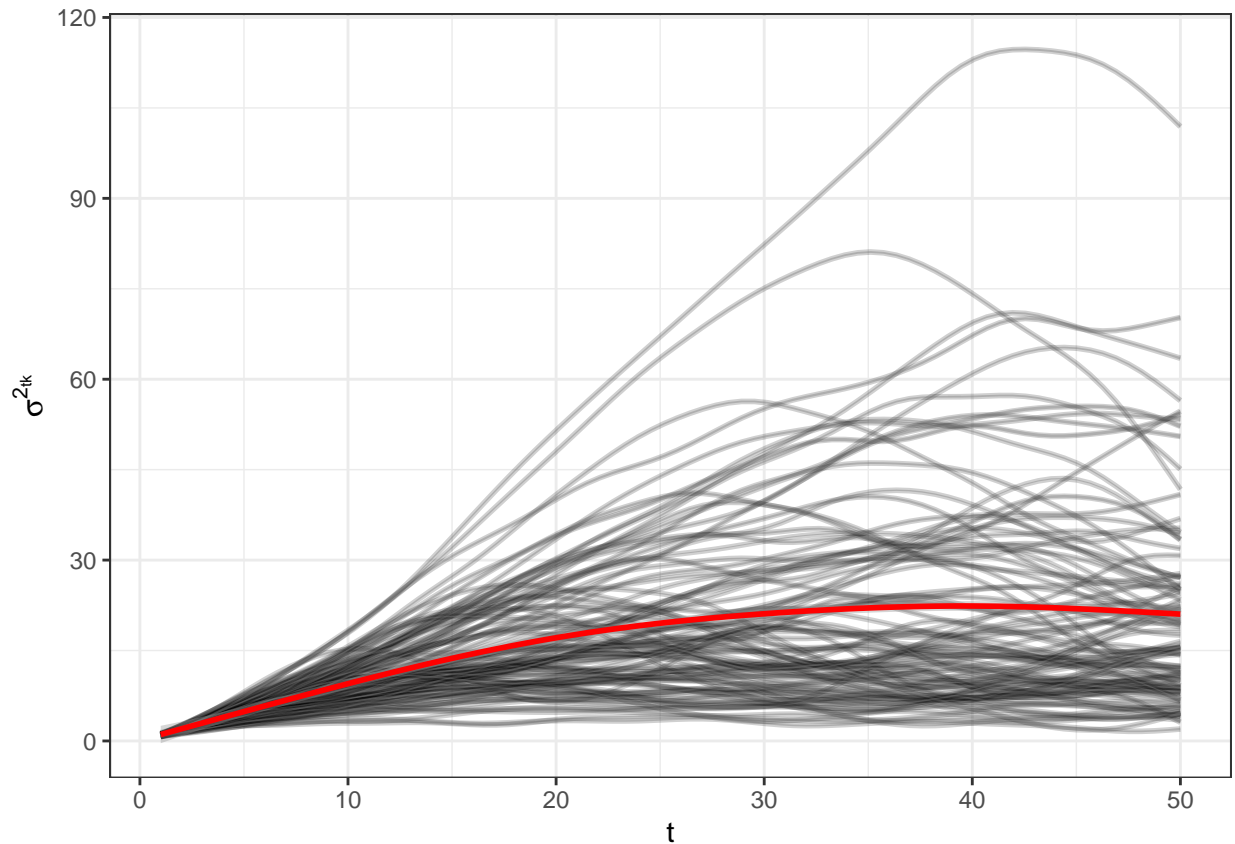


```
x <- expand_grid(t = 1:n,
                 i = 1:100) %>%
  group_by(i) %>%
  mutate(x = cumsum(rnorm(n, sd = 1)),
         var_tk = purrr::map_dbl(t, \(k) var(x - lag(x, k), na.rm = TRUE)))

ggplot(x) +
  geom_smooth(aes(t, var_tk, group = i), method = 'gam',
             formula = y ~ s(x, k = 20), color = '#00000030') +
  geom_smooth(aes(t, var_tk), method = 'gam',
             formula = y ~ s(x, k = 20), color = 'red') +
  xlim(c(NA, n/2)) + # 2nd half of a variogram is not useful
  ylab(expression(sigma^2[tk]))
```

```
## Warning: Removed 5000 rows containing non-finite values (stat_smooth).
```


Warning: Removed 5000 rows containing non-finite values (stat_smooth).



2.2.3 Frontiers Hierarchical, Memory-Based Movement Models for Translocated Elk (*Cervus canadensis*) Ecology and Evolution

Refs to check:

- humans, nonhuman primates and other large-brained vertebrates make movement decisions based on spatial representations of their environments (<https://www.frontiersin.org/articles/10.3389/fevo.2021.702925/#B50>)
- 2010). These representations may allow animals to move directly to important sites in their environment that lie outside of their perceptual range (<https://www.frontiersin.org/articles/10.3389/fevo.2021.702925/#B40>, <https://www.frontiersin.org/articles/10.3389/fevo.2021.702925/#B35>)
- Attribute memory, i.e., non-spatial memory, e.g., food type and abundance (<https://www.frontiersin.org/articles/10.3389/fevo.2021.702925/#B13>)
- Bison remember valuable information about the location and quality of meadows (spatial and attribute memory) and use this information to revisit profitable locations (<https://www.frontiersin.org/articles/10.3389/fevo.2021.702925/#B29>)

- Roe deer an spatial memory for foraging in absence of territoriality (<https://www.frontiersin.org/articles/10.3389/fevo.2021.702925/#B41>)
- memory in capuchin monkeys (<https://www.frontiersin.org/articles/10.3389/fevo.2021.702925/#B8>)
- memory in bison (<https://www.frontiersin.org/articles/10.3389/fevo.2021.702925/#B18>)
- memory in sheep (<https://www.frontiersin.org/articles/10.3389/fevo.2021.702925/#B18>)
- memory in woodland caribou (<https://www.frontiersin.org/articles/10.3389/fevo.2021.702925/#B1>)
- memory in chimpanzees (<https://www.frontiersin.org/articles/10.3389/fevo.2021.702925/#B20>)
- memory constitutes an important mechanism for home range emergence (<https://www.frontiersin.org/articles/10.3389/fevo.2021.702925/#B6>, Börger et al., 2008; Van Moorter et al., 2009)

2.3 Movement types

2.3.1 Range residency

2.3.2 Seasonal migration

2.3.3 Nomadism

predation is more stochastic than herbivory; predators need to match more cycles, depend on less individuals
-> more variable food

Teitelbaum & Mueller (2019): - **Nomadic movement**: with irregular timing and/or direction, producing both within-year and between-year variability in location and movement patterns - **Nomadic movement** is not the same as **migration**, because migration is predictable and cyclical while nomadism is random in time and space - “Data from recent developments in animal tracking technology (e.g., longer-lasting and lighter GPS devices) show that species previously considered migrants or range residents can show irregular, often long-distance, movement patterns (flexible foraging movements of leatherback turtles across the north atlantic ocean, To migrate, stay put, or wander Varied movement strategies in bald eagles, Big data analyses reveal patterns and drivers of the movements of southern elephant seals)”

2.3.4 Edge dynamics

2.4 Two-eyed seeing: Recognizing Traditional Indigenous Knowledge

The ancestral and traditional Knowledge of Indigenous and colonized Peoples is often dismissed, ignored, and contradicted by Western institutions (Smith, 2012). ... The development of Western science is often assumed to clash with the sacred Knowledge many colonized People hold. Western science is also often viewed as more objective, methodical, and unbiased than traditional Knowledge, and as such it is believed

by Western institutions to be superior to Indigenous Knowledge (Smith, 2012). However, it is common for Western institutions to (reluctantly) reach similar, if not identical, conclusions as those held by Indigenous people (ref?). The refusal to recognize traditional Knowledge and cooperate with non-Western institutions often results in a loss of time, resources, and funds to the Western institutions and severe damage to the Land the institution operated on, as well as to the people who's ancestors inhabited the region for millennia. The development of Western science at the exclusion of Indigenous Peoples perpetuates colonialism and brings harm all parties involved.

The concept of *two-eye seeing* (ref?) refers to an approach to knowledge and growth that braids Indigenous Knowledge and science together with Western science (Kutz & Tomaselli, 2019; Kimmerer, 2020). Since Traditional Indigenous Knowledge tends to be qualitative, while biological sciences tend to be quantitative, connecting the two is not always simple. One possibility, however, is to use Traditional Knowledge to create well-informed Bayesian priors (ref?). The validity of the priors can be ensured using prior predictive modeling to select priors that align with the Traditional Knowledge. This practice is not new (Girondot & Rizzo, 2015; Bélisle *et al.*, 2018), but it is rarely used, despite it aligning well with the philosophy of Bayesian statistics.

- Inform priors and simulation distributions using Indigenous Traditional Knowledge:
- A Bayesian framework with Indigenous Knowledge-informed priors (Girondot & Rizzo, 2015)
- *Local knowledge in ecological modeling* (Bélisle *et al.*, 2018)
- <https://focus.science.ubc.ca/stats-660805dd930a>
- *A-spatial-overview-of-the-global-importance-of-Indigenous-lands-for-conservation*
- *Native knowledge for native ecosystems*
- *Searching for synergy integrating traditional and scientific ecological knowledge in environmental science education*
- *The Role of Indigenous Burning in Land Management*
- calls to action for scientists: Wong *et al.* (2020)
- weaving TIK and Western knowledge: Tengö *et al.* (2017)
- *Weaving Indigenous knowledge systems and Western sciences in terrestrial research, monitoring and management in Canada: A protocol for a systematic map* (Henri *et al.*, 2021)
- *Indigenizing the North American Model of Wildlife Conservation* (Hessami *et al.*, 2021)

- fish conservation, Indigenous perspectives (Bowles *et al.*, 2021)
- Vertebrate biodiversity in Indigenous-managed lands in Australia, Brazil, and Canada is equal to or greater biodiversity in protected areas (Schuster *et al.*, 2019)

2.5 Simulations

Look at mechanistic models & energetics

Include:

- effects of animal mass,
- resistance to/ease of movement (e.g., wolves and clear-cut gas lines)
- “state-space model” with 2 spaces: within a patch (slow-moving) and between patches (faster movement)

See R packages for meta-community simulations

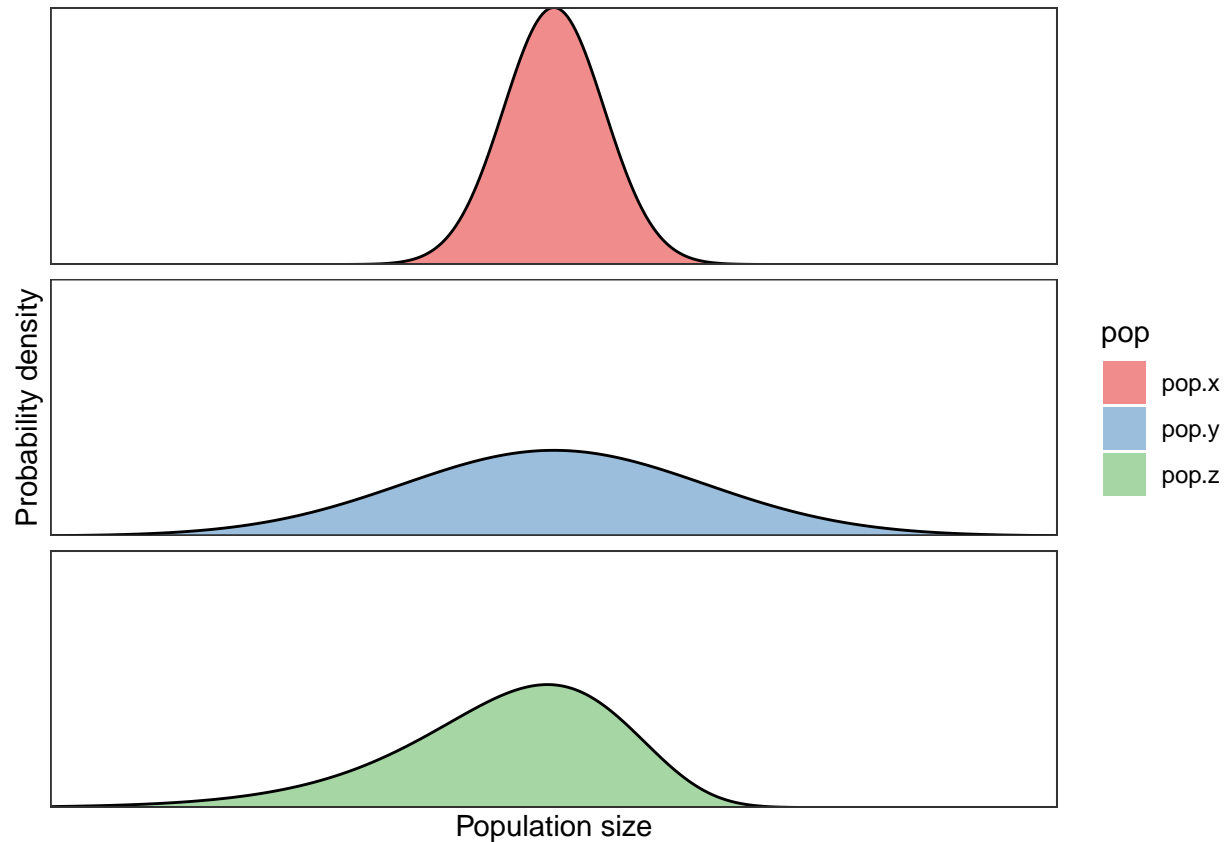
2.5.1 Extreme events and population stability

Figures adapted from a presentation from a presentation I gave on extreme events and mammals for an undergrad course (BIOL385):

```
# density plots ---
d.dens <-
  tibble(x = seq(10, 20, length.out = 400),
         pop.x = dnorm(x, mean = 15, sd = 0.5),
         pop.y = dnorm(x, mean = 15, sd = 1.5),
         pop.z = dweibull(x, 15.53, 15)) %>%
  pivot_longer(cols = c('pop.x', 'pop.y', 'pop.z'), names_to = 'pop', values_to = 'p')

# populations with same means but different shapes and variances
ggplot(d.dens) +
  facet_grid(pop ~ .) +
  geom_ribbon(aes(x, ymin = 0, ymax = p, fill = pop), alpha = 0.5) +
  geom_line(aes(x, p)) +
  geom_hline(yintercept = 0) +
  labs(x = 'Population size', y = 'Probability density') +
```

```
scale_fill_brewer(type = 'qual', palette = 6, direction = 1) +
scale_x_continuous(breaks = NULL, expand = c(0, 0)) +
scale_y_continuous(breaks = NULL, expand = c(0, 0)) +
theme(strip.text = element_blank(), line = element_line(size = .5))
```



```
library('mgcv') # for semi-parametric GAMs
```

```
## Loading required package: nlme
```

```
##
```

```
## Attaching package: 'nlme'
```

```
## The following object is masked from 'package:dplyr':
```

```
##
```

```
## collapse
```

```
## This is mgcv 1.8-38. For overview type 'help("mgcv-package")'.
```

```

library('qgam') # for non-parametric quantile GAMs
library('dplyr') # for data wrangling
theme_set(theme_bw() +
  theme(legend.position = 'none', strip.text = element_blank()))

# simulate population data
d <- tibble(Year = 1500:2050,
  N = c(100, rep(NA, length(Year) - 1)),
  die.off = NA,
  extreme = NA_real_)

# should change the simulation to something more realistic
set.seed(1)
for(i in 2:nrow(d)) { # for each row after the first one
  if(d$N[i - 1] > 1) { # if more than one animal existed in the previous row

    d$N[i] <- d$N[i - 1] - rpois(n = 1, 3) + 3

    # extreme event
    if(d$Year[i] > 1900 & rbinom(1, size = 1, prob = (d$Year[i] / 20000)^2)) {
      d$N[i] <- d$N[i - 1] - rpois(n = 1, lambda = 25)
      d$extreme[i] <- d$Year[i]
    }

    # size <- abs(round(rnorm(1, sd = (d$Year[i] / 1900)^5) / 5)) # magnitude of dieoff
    # d$die.off[i] <- size * ((d$Year[i] - 1800) / 20)^1.5
    # d$N[i] <- d$N[i] - d$die.off[i]

  } else {
    d$N[i - 1] <- 0
    d$N[i] <- 0
  }
}

```

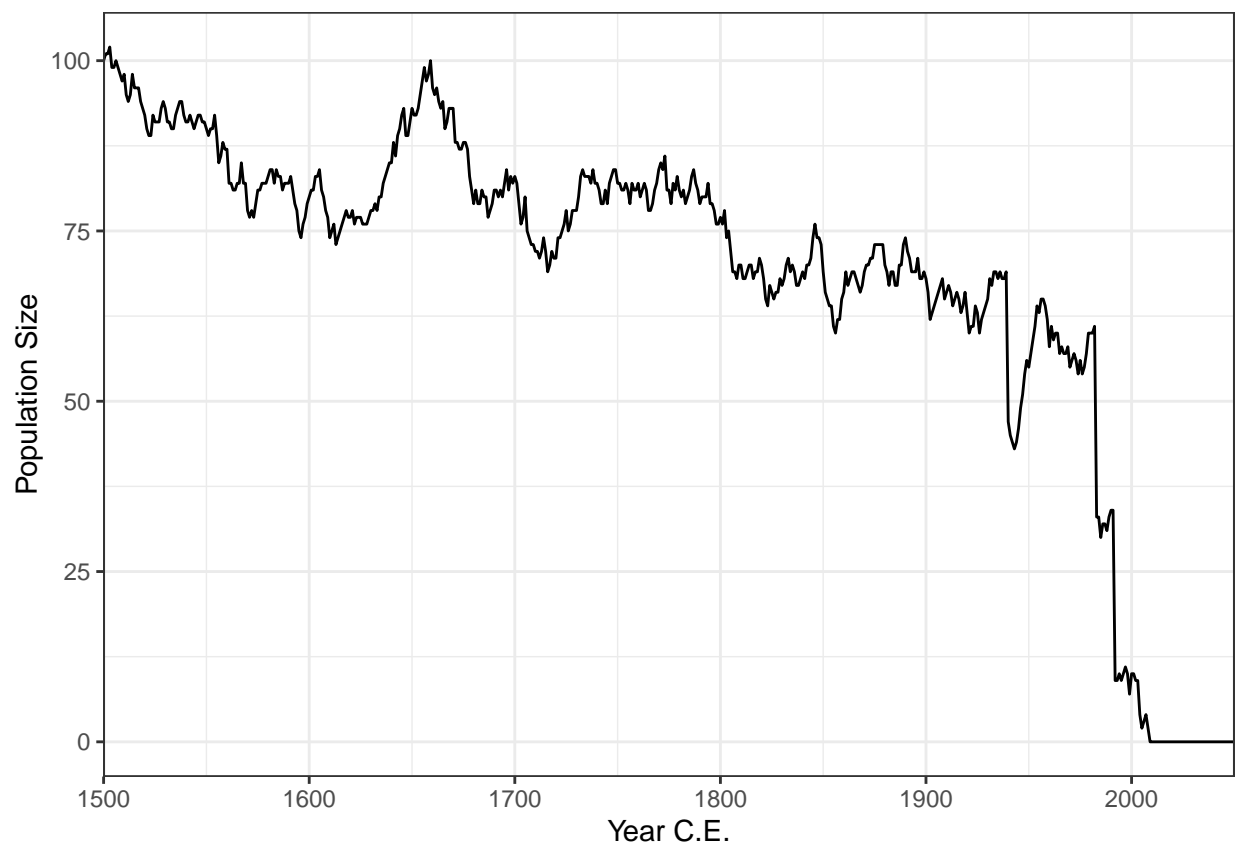
```

}

# reduce population size by ten but keep to a min of 0
# d$N <- if_else(d$N > 5, round(d$N - 5), 0)

ggplot(d, aes(Year, N)) +
  geom_line() +
  scale_x_continuous(expand = c(0, 0)) +
  labs(y = 'Population Size', x = 'Year C.E.')

```



```

# death and birth rates are arbitrary
m0 <- qgam(N ~ s(Year, k = 25), d, qu = .5)

## Estimating learning rate. Each dot corresponds to a loss evaluation.
## qu = 0.5.....done

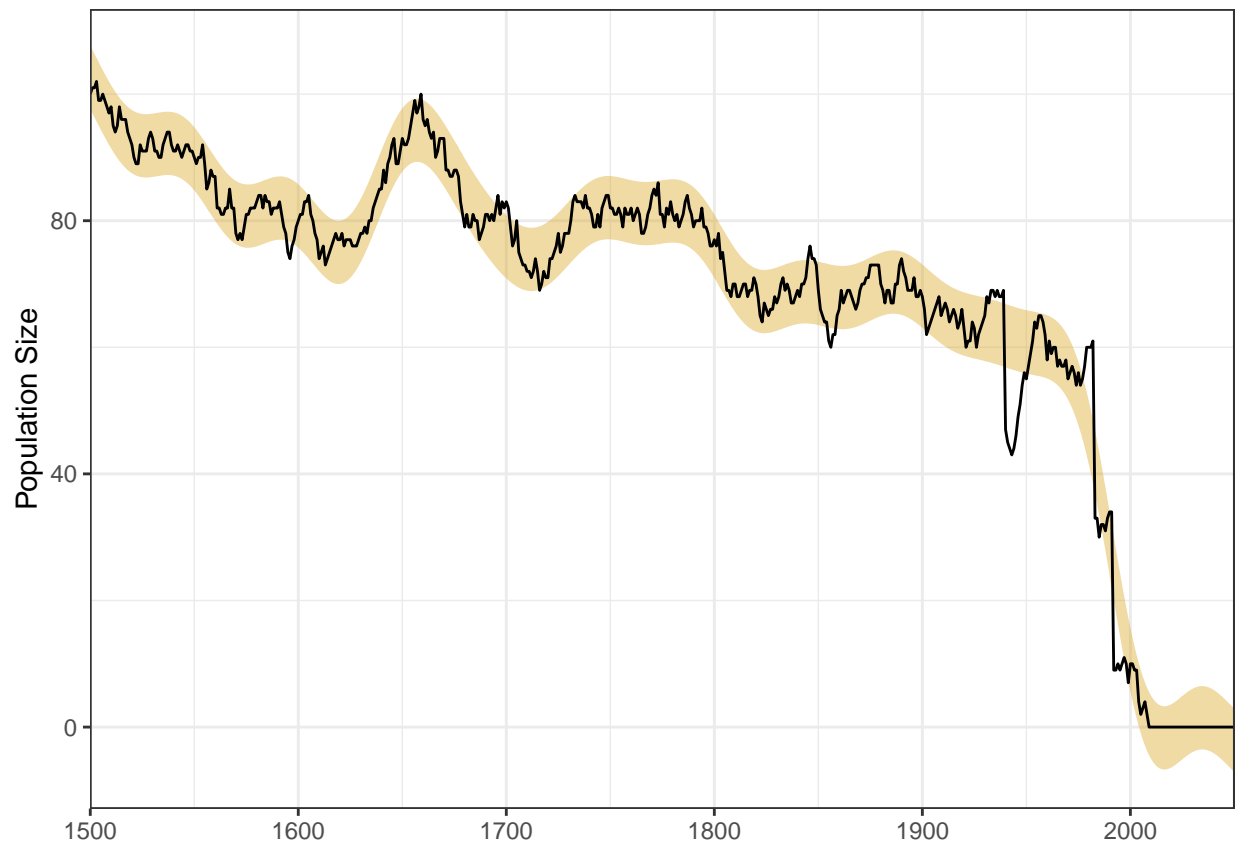
```

```

mu <- predict(m0, type = 'response')
xtrm.lwr <- mu - 5 # lower threshold for extremes
xtrm.upr <- mu + 5 # upper threshold for extremes

# create an arbitrary range for "normal" population levels
ggplot(d, aes(Year, N)) +
  geom_ribbon(aes(ymin = xtrm.lwr, ymax = xtrm.upr), fill = 'goldenrod', alpha = 0.4) +
  geom_line(lwd = .5) +
  scale_x_continuous(expand = c(0, 0)) +
  labs(y = 'Population Size', x = NULL)

```



```

# frequency of unusually high (triangles) or low (crosses) numbers
ggplot(d, aes(Year, N)) +
  geom_ribbon(aes(ymin = xtrm.lwr, ymax = xtrm.upr), fill = 'goldenrod', alpha = 0.4) +
  geom_point(alpha = .5) +
  geom_point(aes(Year, max(d$N) * 1.1), filter(d, N > xtrm.upr),

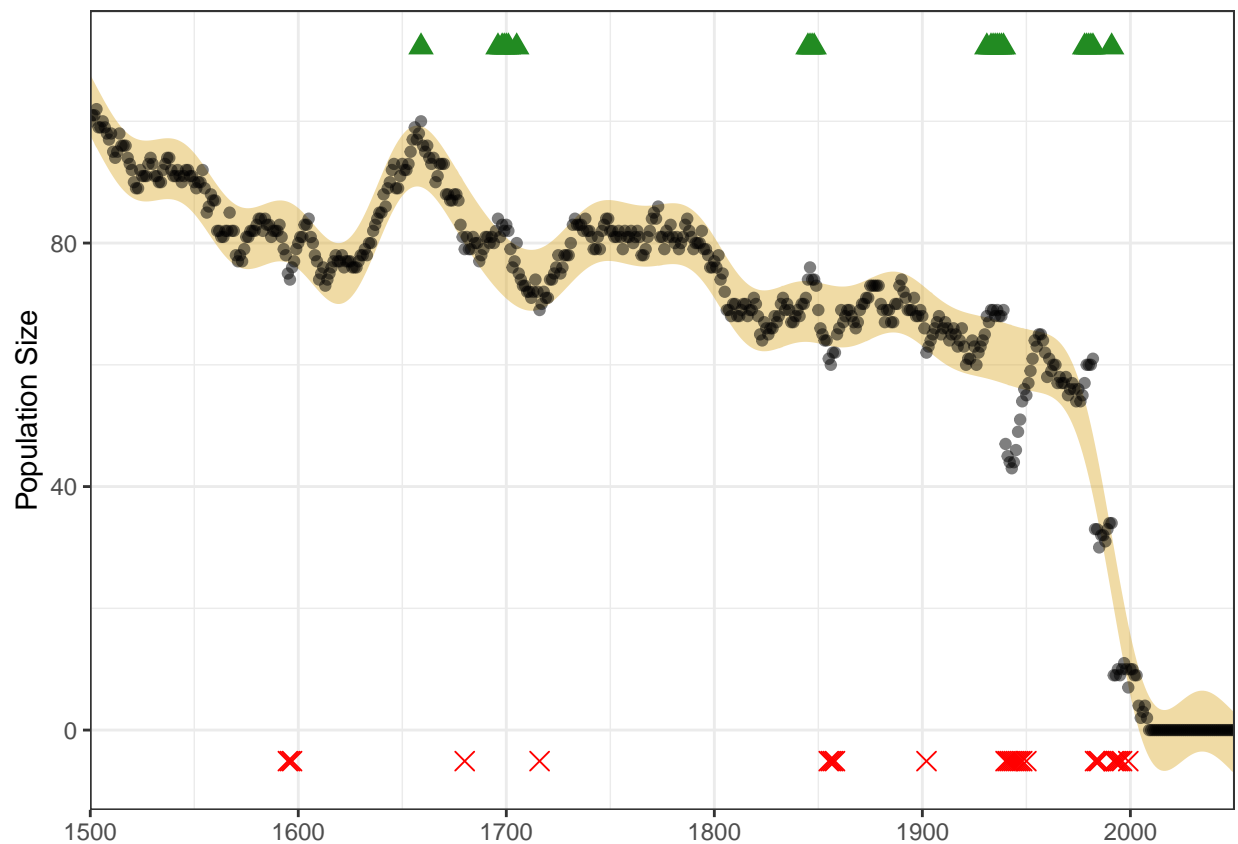
```



```

    col = 'forestgreen', size = 3, shape = 17) +
  geom_point(aes(Year, 0 - max(d$N) * 0.05), filter(d, N < xtrm.lwr),
    col = 'red', size = 3, shape = 4) +
  scale_x_continuous(expand = c(0, 0)) +
  labs(y = 'Population Size', x = NULL)

```



```

# models ----
# LM fails to detect changes in variance and expects linear, monotonic trends
ggplot(d, aes(Year, N)) +
  geom_point(alpha = .5) +
  geom_point(aes(x = extreme, y = - 1), d, color = 'red', pch = 4) +
  geom_smooth(method = 'lm', se = FALSE, formula = y ~ x) +
  labs(y = 'Population Size', x = NULL)

```

```
## Warning: Removed 548 rows containing missing values (geom_point).
```



```
# quantile GAM
```

```
mq <- mqgam(N ~ s(Year, k = 10, bs = 'ad'), data = d,
            qu = c(0.01, 0.99), multicore = TRUE, ncores = 4)
```

```
## Estimating learning rate. Each dot corresponds to a loss evaluation.
```

```
## qu = 0.01.....done
```

```
## qu = 0.99.....done
```

```
pred.q <-
```

```
  tibble(Year = d$Year,
         N.99 = qdo(mq, qu = c(0.99),
                    \ (m) predict(m, newdata = tibble(Year = Year))),
         N.01 = qdo(mq, qu = c(0.01),
                    \ (m) predict(m, newdata = tibble(Year = Year))))
```

```
# quantile GAM (or location-scale GAM) can detect change in
```

```
ggplot(pred.q) +
```

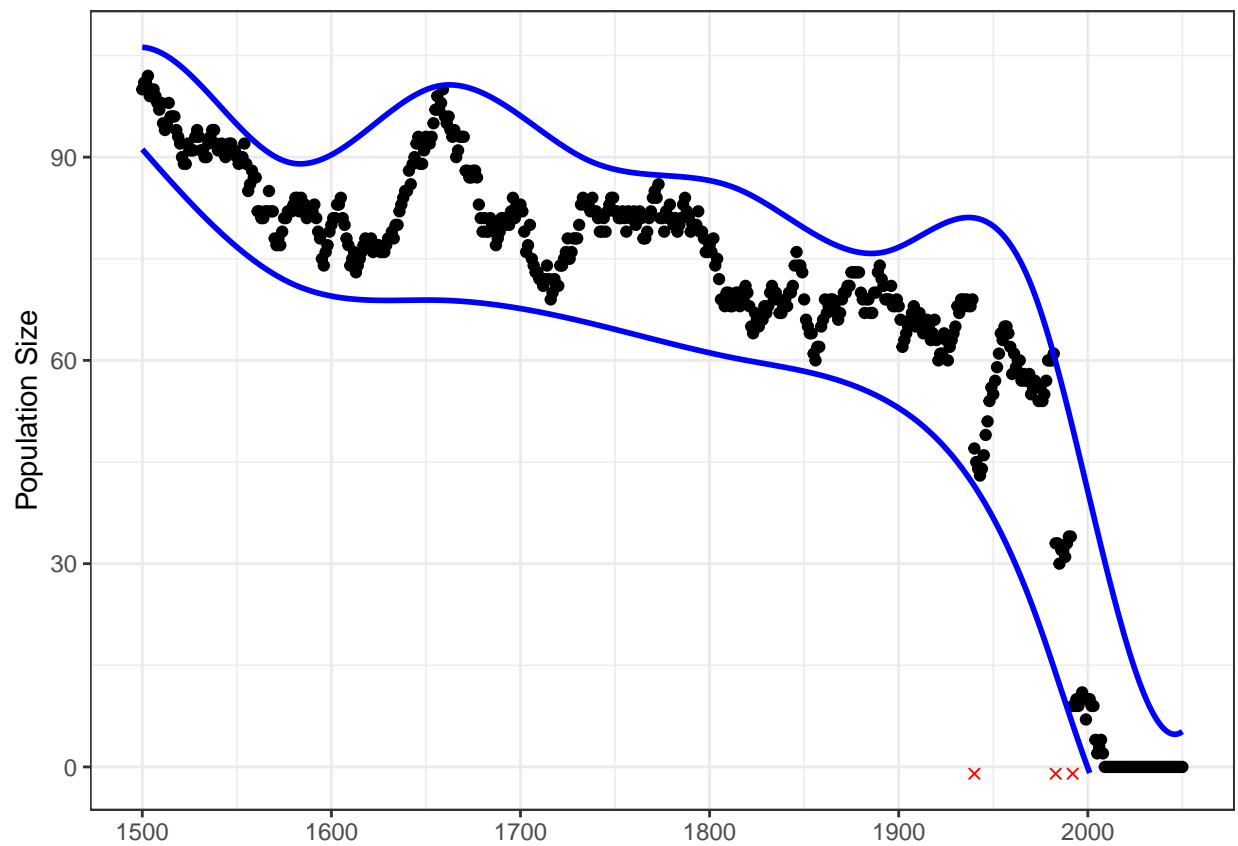
```

geom_point(aes(Year, N), d) +
geom_point(aes(x = extreme, y = - 1), d, color = 'red', pch = 4) +
geom_line(aes(Year, N.99), col = 'blue', lwd = 1) +
geom_line(aes(Year, N.01), col = 'blue', lwd = 1) +
ylim(c(-1, NA)) +
labs(y = 'Population Size', x = NULL)

```

```
## Warning: Removed 548 rows containing missing values (geom_point).
```

```
## Warning: Removed 49 row(s) containing missing values (geom_path).
```



3 Chapter 2: A new measure of environmental stochasticity

quantify levels and stability of green light wave (see NDVI) with and without human modification/activity,
include citizen science data (e.g., flowering phenology)

4 Chapter 3: Movement analyses

4.1 Movement simulations

- Inform priors and simulation distributions using Indigenous Traditional Knowledge

4.2 Stochasticity map

- currently there's no raster of stochasticity => paper / product
- PCA on main drivers/causes of stochasticity

4.3 Movement analysis

4.3.1 Model types

- add HFI to analysis (but it's temporally static)
- define and describe:
 - IID model
 - OU anisotropic, isotropic
 - OUF anisotropic, isotropic,
 - OUf anisotropic
- look at HPAMs?

5 Project timeline

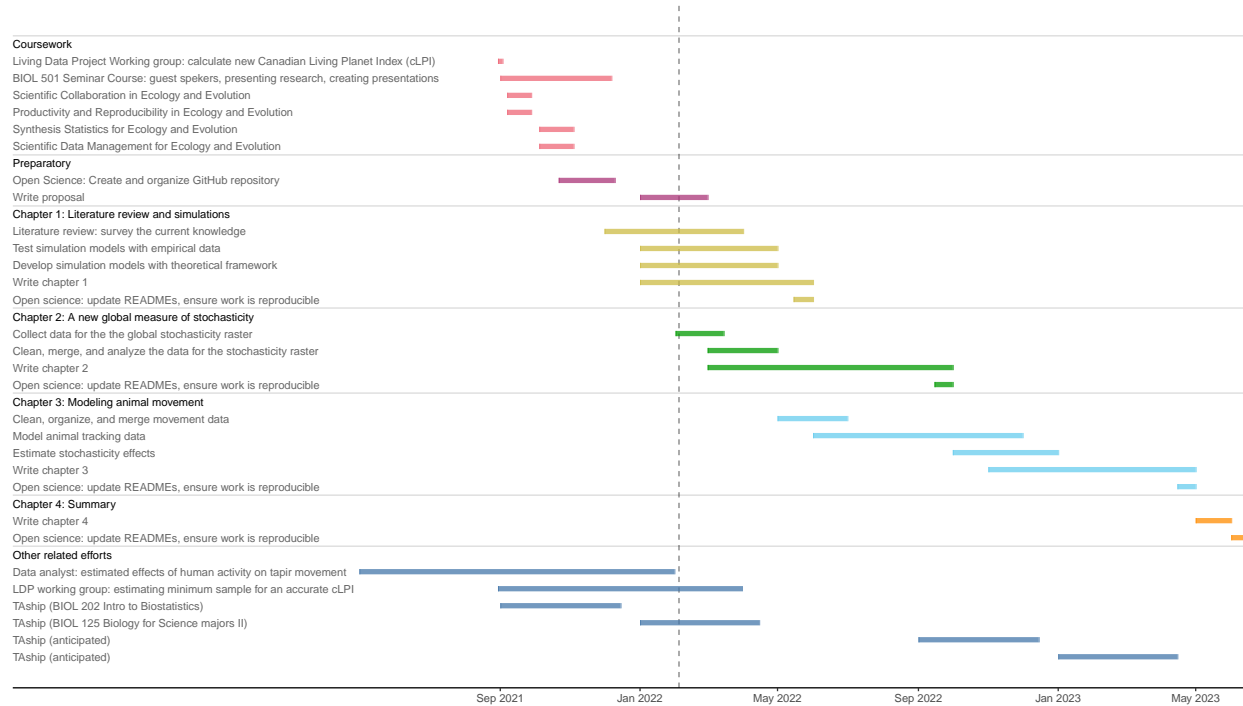


Figure 8: Visual representation of the estimated timeline for my Master's project.

6 Chapter 4: Summary

7 Conclusion

- why is this work important?
- so what?
- now what?

8 List of abbreviations

Abbreviation	Phrase
CTMM	Continuous-time movement model
GAM	Generalized additive model
HGAM	Hierarchical generalized additive model
HR	Home range

9 Progress to date

Bibliography

- Bachmaier M. & Backes M. (2011). Variogram or Semivariogram? Variance or Semivariance? Allan Variance or Introducing a New Term? *Mathematical Geosciences* **43**, 735–740. <https://doi.org/10.1007/s11004-011-9348-3>
- Bélisle A.C., Asselin H., LeBlanc P. & Gauthier S. (2018). Local knowledge in ecological modeling. *Ecology and Society* **23**, art14. <https://doi.org/10.5751/ES-09949-230214>
- Bell G., Lechowicz M.J., Appenzeller A., Chandler M., DeBlois E., Jackson L., *et al.* (1993). The spatial structure of the physical environment. *Oecologia* **96**, 114–121. <https://doi.org/10.1007/BF00318038>
- Blackwell P.G. (2007). Heterogeneity, patchiness and correlation of resources. *Ecological Modelling* **207**, 349–355. <https://doi.org/10.1016/j.ecolmodel.2007.05.012>
- Bolstad W.M. & Curran J.M. (2017). *Introduction to Bayesian statistics*, Third edition. Wiley, Hoboken, New Jersey.
- Bowles E., Marin K., MacLeod P. & Fraser D.J. (2021). A three-pronged approach that leans on Indigenous knowledge for northern fish monitoring and conservation. *Evolutionary Applications* **14**, 653–657. <https://doi.org/10.1111/eva.13146>
- Burt W.H. (1943). Territoriality and Home Range Concepts as Applied to Mammals. *Journal of Mammalogy* **24**, 346. <https://doi.org/10.2307/1374834>
- Chevin L.-M., Lande R. & Mace G.M. (2010). Adaptation, Plasticity, and Extinction in a Changing Environment: Towards a Predictive Theory. *PLoS Biology* **8**, e1000357. <https://doi.org/10.1371/journal.pbio.1000357>
- DeSoto L., Cailleret M., Sterck F., Jansen S., Kramer K., Robert E.M.R., *et al.* (2020). Low growth resilience to drought is related to future mortality risk in trees. *Nature Communications* **11**, 545. <https://doi.org/10.1038/s41467-020-14300-5>
- Dickie M., Serrouya R., Avgar T., McLoughlin P., McNay R.S., DeMars C., *et al.* Resource exploitation efficiency collapses the home range of an apex predator. *Ecology*. <https://doi.org/10.1002/ecy.3642>
- Fahrig L. (2007). Non-optimal animal movement in human-altered landscapes. *Functional Ecology* **21**, 1003–1015. <https://doi.org/10.1111/j.1365-2435.2007.01326.x>
- Falcón-Cortés A., Boyer D., Merrill E., Frair J.L. & Morales J.M. (2021). Hierarchical, Memory-Based Movement Models for Translocated Elk (*Cervus canadensis*). *Frontiers in Ecology and Evolution* **9**, 702925. <https://doi.org/10.3389/fevo.2021.702925>
- Foley C., Pettorelli N. & Foley L. (2008). Severe drought and calf survival in elephants. *Biology Letters* **4**, 541–544. <https://doi.org/10.1098/rsbl.2008.0370>

- Girondot M. & Rizzo A. (2015). Bayesian Framework to Integrate Traditional Ecological Knowledge into Ecological Modeling: A Case Study. *Journal of Ethnobiology* **35**, 337–353. <https://doi.org/10.2993/etbi-35-02-337-353.1>
- Government of Canada (2021). *Canadian Protected and Conserved Areas Database*.
- Grant J.W.A. (1993). Whether or not to defend? The influence of resource distribution. *Marine Behaviour and Physiology* **23**, 137–153. <https://doi.org/10.1080/10236249309378862>
- Haig H.A., Kingsbury M.V., Laird K.R., Leavitt P.R., Laing R. & Cumming B.F. (2013). Assessment of drought over the past two millennia using near-shore sediment cores from a Canadian boreal lake. *Journal of Paleolimnology* **50**, 175–190. <https://doi.org/10.1007/s10933-013-9712-z>
- Hansen M.C., Potapov P.V., Moore R., Hancher M., Turubanova S.A., Tyukavina A., *et al.* (2013). High-Resolution Global Maps of 21st-Century Forest Cover Change. *Science* **342**, 850–853. <https://doi.org/10.1126/science.1244693>
- Henri D.A., Provencher J.F., Bowles E., Taylor J.J., Steel J., Chelick C., *et al.* (2021). Weaving Indigenous knowledge systems and Western sciences in terrestrial research, monitoring and management in Canada: A protocol for a systematic map. *Ecological Solutions and Evidence* **2**. <https://doi.org/10.1002/2688-8319.12057>
- Hessami M.A., Bowles E., Popp J.N. & Ford A.T. (2021). Indigenizing the North American Model of Wildlife Conservation. *FACETS* **6**, 1285–1306. <https://doi.org/10.1139/facets-2020-0088>
- IPCC (2018). *Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty*.
- Johnson D.S., London J.M., Lea M.-A. & Durban J.W. (2008). Continuous-time correlated random walk model for animal telemetry data. *Ecology* **89**, 1208–1215. <https://doi.org/10.1890/07-1032.1>
- Jonzén N., Lindén A., Ergon T., Knudsen E., Vik J.O., Rubolini D., *et al.* (2006). Rapid Advance of Spring Arrival Dates in Long-Distance Migratory Birds. *Science* **312**, 1959–1961. <https://doi.org/10.1126/science.1126119>
- Kimmerer R.W. (2020). *Braiding sweetgrass: Indigenous wisdom, scientific knowledge, and the teachings of plants*, Second hardcover edition. Milkweed Editions, Minneapolis.
- Kolasa J., Hewitt C.L. & Drake J.A. (1998). Rapoport’s rule: An explanation or a byproduct of the latitudinal gradient in species richness? *Biodiversity and Conservation* **7**, 1447–1455. <https://doi.org/10.1023/A:1008805230673>
- Kutz S. & Tomaselli M. (2019). “Two-eyed seeing” supports wildlife health. *Science* **364**, 1135–1137.

<https://doi.org/10.1126/science.aau6170>

- Lindstedt S.L. & Boyce M.S. (1985). Seasonality, Fasting Endurance, and Body Size in Mammals. *The American Naturalist* **125**, 873–878. <https://doi.org/10.1086/284385>
- Lucherini M. & Lovari S. (1996). Habitat richness affects home range size in the red fox *Vulpes vulpes*. *Behavioural Processes* **36**, 103–105. [https://doi.org/10.1016/0376-6357\(95\)00018-6](https://doi.org/10.1016/0376-6357(95)00018-6)
- Morellet N., Bonenfant C., Börger L., Ossi F., Cagnacci F., Heurich M., *et al.* (2013). Seasonality, weather and climate affect home range size in roe deer across a wide latitudinal gradient within Europe. *Journal of Animal Ecology* **82**, 1326–1339. <https://doi.org/10.1111/1365-2656.12105>
- Nandintsetseg D., Bracis C., Leimgruber P., Kaczensky P., Buuveibaatar B., Lkhagvasuren B., *et al.* (2019). Variability in nomadism: Environmental gradients modulate the movement behaviors of dryland ungulates. *Ecosphere* **10**. <https://doi.org/10.1002/ecs2.2924>
- Nilsen E.B., Herfindal I. & Linnell J.D.C. (2005). Can intra-specific variation in carnivore home-range size be explained using remote-sensing estimates of environmental productivity? *Écoscience* **12**, 68–75. <https://doi.org/10.2980/i1195-6860-12-1-68.1>
- Pedersen E.J., Miller D.L., Simpson G.L. & Ross N. (2019). Hierarchical generalized additive models in ecology: An introduction with mgcv. *PeerJ* **7**, e6876. <https://doi.org/10.7717/peerj.6876>
- R Core Team (2021). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Relyea R.A., Lawrence R.K. & Demarais S. (2000). Home Range of Desert Mule Deer: Testing the Body-Size and Habitat-Productivity Hypotheses. *The Journal of Wildlife Management* **64**, 146. <https://doi.org/10.2307/3802984>
- Rickbeil G.J.M., Merkle J.A., Anderson G., Atwood M.P., Beckmann J.P., Cole E.K., *et al.* (2019). Plasticity in elk migration timing is a response to changing environmental conditions. *Global Change Biology* **25**, 2368–2381. <https://doi.org/10.1111/gcb.14629>
- Riotte-Lambert L. & Matthiopoulos J. (2020). Environmental Predictability as a Cause and Consequence of Animal Movement. *Trends in Ecology & Evolution* **35**, 163–174. <https://doi.org/10.1016/j.tree.2019.09.009>
- Roche D.G., Kruuk L.E.B., Lanfear R. & Binning S.A. (2015). Public Data Archiving in Ecology and Evolution: How Well Are We Doing? *PLOS Biology* **13**, e1002295. <https://doi.org/10.1371/journal.pbio.1002295>
- Ryan Patrick Jones (2021). PM commits up to \$55 million to reduce land degradation at virtual biodiversity summit. *CBC News*
- Schuster R., Germain R.R., Bennett J.R., Reo N.J. & Arcese P. (2019). Vertebrate biodiversity on

- indigenous-managed lands in Australia, Brazil, and Canada equals that in protected areas. *Environmental Science & Policy* **101**, 1–6. <https://doi.org/10.1016/j.envsci.2019.07.002>
- Smith L.T. (2012). *Decolonizing methodologies: Research and indigenous peoples*, Second edition. Zed Books, London.
- Southwood T.R.E. (1977). Habitat, the Templet for Ecological Strategies? *The Journal of Animal Ecology* **46**, 336. <https://doi.org/10.2307/3817>
- Stanton K.M., Weeks S.S., Dana M.N. & Mickelbart M.V. (2010). Light Exposure and Shade Effects on Growth, Flowering, and Leaf Morphology of *Spiraea alba* Du Roi and *Spiraea tomentosa* L. *HortScience* **45**, 1912–1916. <https://doi.org/10.21273/HORTSCI.45.12.1912>
- Teitelbaum C.S. & Mueller T. (2019). Beyond Migration: Causes and Consequences of Nomadic Animal Movements. *Trends in Ecology & Evolution* **34**, 569–581. <https://doi.org/10.1016/j.tree.2019.02.005>
- Tengö M., Hill R., Malmer P., Raymond C.M., Spierenburg M., Danielsen F., *et al.* (2017). Weaving knowledge systems in IPBES, CBD and beyond—lessons learned for sustainability. *Current Opinion in Environmental Sustainability* **26–27**, 17–25. <https://doi.org/10.1016/j.cosust.2016.12.005>
- Truth and Reconciliation Commission of Canada (2015). *Honouring the truth, reconciling for the future: Summary of the final report of the Truth and Reconciliation Commission of Canada*. Truth; Reconciliation Commission of Canada.
- Tucker M.A., Böhning-Gaese K., Fagan W.F., Fryxell J.M., Van Moorter B., Alberts S.C., *et al.* (2018). Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science* **359**, 466–469. <https://doi.org/10.1126/science.aam9712>
- Wilson M.C., Chen X.-Y., Corlett R.T., Didham R.K., Ding P., Holt R.D., *et al.* (2016). Habitat fragmentation and biodiversity conservation: Key findings and future challenges. *Landscape Ecology* **31**, 219–227. <https://doi.org/10.1007/s10980-015-0312-3>
- Wolkovich E.M., Cook B.I., Allen J.M., Crimmins T.M., Betancourt J.L., Travers S.E., *et al.* (2012). Warming experiments underpredict plant phenological responses to climate change. *Nature* **485**, 494–497. <https://doi.org/10.1038/nature11014>
- Wong C., Ballegooyen K., Ignace L., Johnson M.J.(Gùdia). & Swanson H. (2020). Towards reconciliation: 10 Calls to Action to natural scientists working in Canada. *FACETS* **5**, 769–783. <https://doi.org/10.1139/facets-2020-0005>
- Wood S.N. (2017). *Generalized additive models: An introduction with R*, Second edition. CRC Press/Taylor & Francis Group, Boca Raton.

Appendix 1

