

**LINKING RESOURCE ABUNDANCE AND ENVIRONMENTAL STOCHASTICITY
WITH ANIMAL SPACE USE USING CONTINUOUS-TIME STOCHASTIC PROCESSES**

by

Stefano Mezzini

B.Sc. Hons. Biology, University of Regina, 2021

B.Sc. Statistics, University of Regina, 2021

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in

THE COLLEGE OF GRADUATE STUDIES

(Biology)

THE UNIVERSITY OF BRITISH COLUMBIA

(Okanagan)

March 2022

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The following individuals certify that they have read, and recommend to the College of Graduate Studies for acceptance, a thesis entitled:

Linking resource abundance and environmental stochasticity with animal space use using continuous-time stochastic processes,

submitted by Stefano Mezzini in partial fulfillment of the requirements of the degree of Master of Science.

Michael J. Noonan _____

Supervisor

Adam T. Ford _____

Supervisory Committee Member

Jason Pither _____

Supervisory Committee Member

University Examiner. _____

University Examiner

External Examiner. _____

External Examiner

Abstract

0.1 Write for proposal, cannot exceed 350 words

Lay Summary

{Not necessary for proposal, but good to have.}

Foreword

Two-eyed seeing: Recognizing Traditional Indigenous Knowledge

The lands managed and protected by Indigenous Peoples are often markedly different from those inhabited by urban societies. While recognizing that there is great diversity between Indigenous Peoples (as well as other colonized Peoples), it is important to recognize that many hold great knowledge on how to live sustainably, safeguard environments, and protect biodiversity (Schuster *et al.*, 2019), and have been doing so for millennia. Yet, their leaders and representatives are seldom included in conservation-related decision-making. Instead, many Western institutions often dismiss, ignore, and contradict the ancestral and traditional Knowledge of Indigenous and colonized Peoples (Smith, 2012). The development of Western science is frequently assumed to clash with the (often sacred) Knowledge many colonized People hold. Western science is often viewed as more objective, methodical, and unbiased than traditional Knowledge, and as such Western institutions and people often consider it 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 (ref?). 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* 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 (Bowles *et al.*, 2021). One possibility, however, is to use Traditional Knowledge to create properly informed Bayesian priors (Bolstad & Curran, 2017). The validity of the priors can be ensured using prior predictive modeling (McElreath, 2016) to select priors that align with the Traditional Knowledge. This practice is not new (Girondot & Rizzo, 2015; Béliele *et al.*, 2018), but it is rarely used, despite it aligning well with the philosophy of Bayesian statistics.

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Acknowledgements

I would like to thank Dr. Noonan for offering me the opportunity to pursue a Master's degree with such an interesting project with cutting-edge statistical methods for movement ecology. I have already learned a lot and I expect I will learn much more.

I would like to thank Dr. Ford and Dr. Pither for agreeing to be on my committee. Your feedback and mentorship will help me ensure this project is relevant and directly applicable to current issues regarding conservation and biogeography.

I would like to thank Sandra Fox for providing me with resources to ensure my perspective and work are inclusive and supportive of different ways of knowing, including Indigenous Knowledge, and that my attitude remains anti-colonial and anti-imperial.

Dedication

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

1 Chapter 1: Literature review and quantitative predictions

1.1 Home ranges as proxies for animals' needs

The ability to move allows most animals to adapt rapidly and continuously to heterogeneous and changing environments. Animals may move to search for resources (e.g., as food, nutrients, water, heat, a new den or nesting spot), a mate, or a new group. Movement also allows animals to escape predation or dangerous competition, and it allows them to defend resources and territory, too. Thus, we can estimate changes in animals' movement and space use as a proxy for many needs, rather than measuring changes in the various individual needs ([ref?](#)).

The concept of a home range (HR) is often used to indicate the space an animal requires to satisfy its essential needs during a period of time (Burt, 1943). Such needs include energetic needs and reproductive needs (which are not limited to finding a mate, since offspring require energy a safe location to develop in, too), but exploratory movement outside the core HR are generally not accounted for. However, for an animal to have what we may consider a HR, the animal must remain in a stable "home" area for long periods of time. That is, the animal must be range-resident and the HR must have a stable centroid. Stable centroids may be concrete locations such as an eagle's nest, a bear's den, or a bee's hive, or they may be abstract points such as the center of a coyote's hunting grounds or the center of a deer's foraging grounds.

While the HR may change over time (e.g., following a forest fire or a flood), it should remain be stable during the period of observation. Ideally, properties of the HR (e.g., range size and crossing time) are representative of any new HR the animal will move to if the current one becomes inhospitable. Thus, animals with an unstable centroid would not be appropriate for HR analysis. Nomadic or migrating animals (e.g., Nandintsetseg *et al.*, 2019) are thus generally not considered range resident, and tracking periods should be long enough to provide a representative sample of the animal's spatial needs.

In the case of a species or population where spatial needs change over the animals' lifetimes (e.g., [ref?](#)), one may define HR as a function of the animal's life stages (with distinct discrete HRs) or as a function of age (so HR changes smoothly). In either case, the accuracy of the estimate will depend strongly on the length of the observation period as well as the measurement frequency. Data from a portion of an animal's life may be sufficient if it is representative the animal's movement or if inference is limited to the period(s) for which data is available (figure 1).

There are many factors which may affect animal's spatial requirements and how they use their HR. Resource abundance is often assumed to be inversely proportional to HR size (or some function of it), such that regions

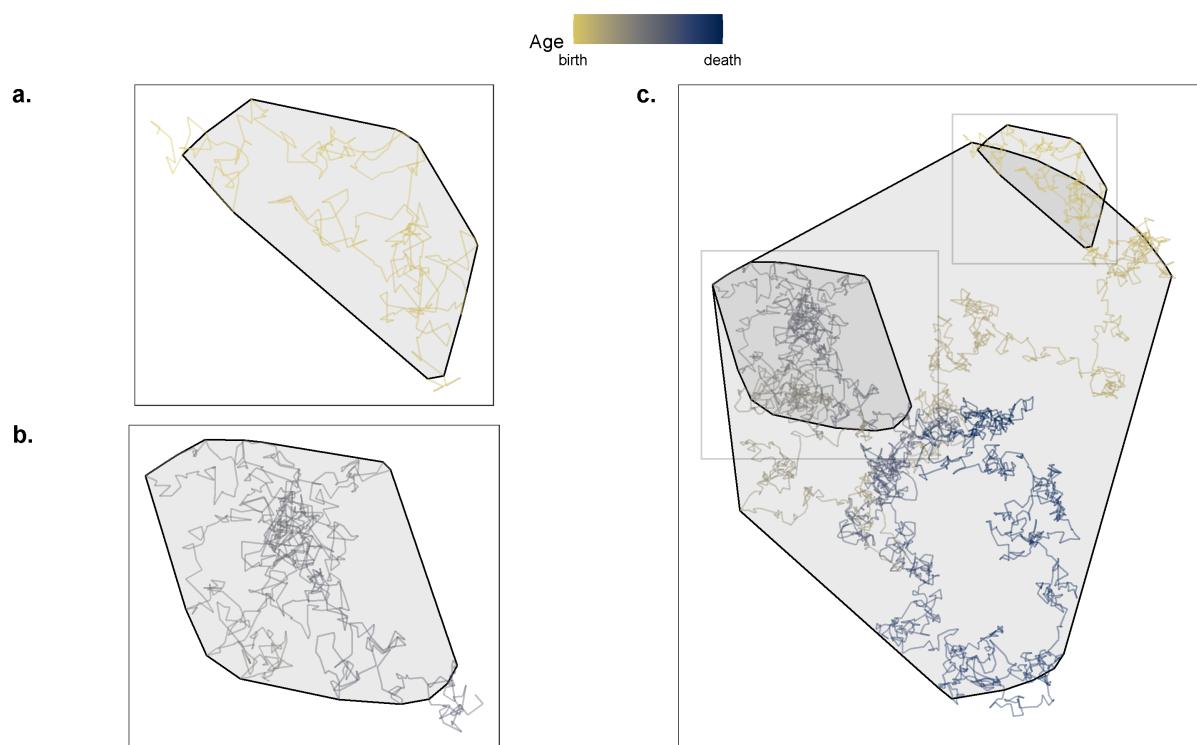


Figure 1: Simulated movement of an individual over their life. Samples from different periods of the animal's life may result in different conclusions, such as slow nomadism (a) or range residency (b), but neither sample is representative of the space the animal used over its entire life (c).

with higher abundance correspond to smaller spatial needs. However, the effect of many other factors likely depends on how an animal responds to them. For instance, competition may push individuals to explore other areas and expand their HR, but strong and consistent competition may also prevent them from doing so. Similarly, predation may force animals to move more frequently to escape predators, or it may prevent them from venturing too far from the safety of their den (the HR's centroid) too often. Fragmentation and patch heterogeneity may cause animals to explore more patches if some are of low value, but high diversity may also decrease HR size (Lucherini & Lovari, 1996). Similarly, patch connectivity and ease of movement may favor exploration and a wider HR (Dickie *et al.* in press), or they may decrease the animal's energetic needs and the HR with it.

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; Lucherini & Lovari, 1996; Nilsen, Herfindal & Linnell, 2005; Bengsen *et al.*, 2016), and supported (or questioned) by more recent work with larger, higher-resolution datasets (e.g., Jonzén *et al.*, 2006; Wolkovich *et al.*, 2012; Falcón-Cortés *et al.*, 2021; Dickie *et al.* in press) and simulations (Blackwell, 2007). Recently, the amount of movement data which can be modeled at once has increased due to improvements in the quality and affordability of tracking equipment (Rutz & Hays, 2009), together with growing propensity (and requirements) to share data openly on various open data platforms such as Movebank (Kranstauber *et al.*, 2011; Kays *et al.*, 2022; but see Roche *et al.*, 2015), as well as the development of high-level modeling software (Bürkner, 2017, 2018; Wood, 2017; e.g., R Core Team, 2021).

It is understood that an animal's spatial use strongly depends on the amount of resources and energy the animal can obtain from their habitat, but estimates are often restricted to single populations or at most single species. To my knowledge, there are currently no large-scale estimations of vertebrate (or mammalian) space use as a function of resource availability. Additionally, little attention is often given to the stochasticity of resource availability or, more generally, habitat heterogeneity and stochasticity (but see Lucherini & Lovari, 1996; Nilsen *et al.*, 2005; Rizzuto *et al.*, 2021). This project aims to quantify the effects of resource abundance and environmental stochasticity on animal space use using statistical models which are based on continuous-time stochastic processes and are insensitive to sampling frequency and spatiotemporal or taxonomic autocorrelation in the data. We hope findings from this project will inform us on how stochasticity has shaped the ecology and evolution of terrestrial mammals and how terrestrial mammals are currently adapting to heterogeneous and changing environments.

1.2 Effects of resource availability and productivity on spatial needs

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 ([refs?](#)), an environment's heterogeneity (i.e., diversity), stochasticity (i.e., unpredictability), 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, decreases animals' fitness. Therefore, I expect animals living in unpredictable environments to require more space than those in stable environments. 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 the extent to which these preliminary findings can be generalized is still very limited. There thus 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; Noonan *et al.*, 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).

Animals' needs vary greatly between taxonomic groups, but some needs are essential for most species for survival and reproduction, such as energetic needs (e.g., food, water; see [ref?](#)), habitat needs (e.g., dens, trees, tall grass, breeding grounds, protection from predators and competitors; see [refs?](#)), and maintaining a thermoregulatory balance. The size of a home range (defined as the area used by an animal to satisfy its essential needs, such as gathering food and resources, mating, and raising offspring), is hypothesized to be proportional to resource abundance (Burt, 1943), such that spatial needs increase 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; Jetz *et al.*, 2004). Home range 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), although the effect human modifications have on animal movement may depend on environmental harshness (Dawe, Bayne & Boutin, 2014). However, not all animals take advantage of linear features or higher predictability in human-altered

habitats. Noonan *et al.* (2021) found that giant anteaters (*Myrmecophaga tridactyla*) in Brazil did not use roads to reduce movement costs or increase movement speed. Instead, roads increased anteater mortality because the animals were attracted to the high-quality foraging found on roadside habitat. Similarly, Medici *et al.* (in press) found that the movement of tapirs (*Tapirus terrestris*) was unaffected by anthropogenic activity or habitat type.

1.3 Effects of environmental heterogeneity and stochasticity on spatial needs

The favorableness of a patch or habitat often depends on a variety of factors, including resource availability, competitive pressure, and predation risk. Let R indicate the amount of *resources* in a particular patch, and let S be the random variable indicating whether or not a patch visit is *successful*. For simplicity, we can let S follow a Bernoulli distribution with probability of success p (which we can write as $S \sim Ber(p)$). Next, let $U = R \cdot S$ indicate the resources an animal can *use* during a visit. Following this simple model, a patch visit can result in two possible outcomes: if the visit is successful ($S = 1$), an animal can use the entirety of the resource ($U = R \cdot 1 = R$), but if it is unsuccessful ($S = 0$) the animal is unable to access any of the resource ($U = R \cdot 0 = 0$).

Let's start by considering the simplistic (and unlikely) scenario where patches are fully predictable and free of disturbance and competition, such that the animal can access the patches' resources during any visit, i.e., $p = P(S = 1) = 1$. In heterogeneous regions with no stochasticity (figure 2a-b), the favorableness of a location will depend strongly on R , so regions with higher R should be preferred (figure 2c). Since all patch visits in fully predictable regions are successful, animals can expect U to be equal to R , since $U = R \cdot S = R \cdot 1 = R$ (figure 2d), which implies that $\mathbb{E}(U) = \mathbb{E}(RS) = \mathbb{E}(R)$. Since $U = R$, animals can choose their home ranges based on R without having to account for any spatiotemporal stochasticity. Therefore, animals in such regions are likely to maximize fitness and minimize movement costs by spending large amounts of time in highly productive regions, with occasional exploratory movements to different patches. This model is quite simplistic, but its simplicity makes it easy to fit and conceptualize. While it is unlikely for a region to be fully predictable, this model may provide acceptable results when environmental variance is low and has little effect on animal fitness, such as in areas where the variation in U , $\mathbb{V}(U)$, is low relative to its expected value, $\mathbb{E}(U)$, such that the costs of moving to another favorable area are low or the chances of encountering prey are high. Mathematically, we can say that this simple model may be acceptable when the coefficient of variation, $\sqrt{\mathbb{V}(R)} / \mathbb{E}(R)$, is low. Additionally, this model may be the only option when data availability is too low to produce appreciable measures of stochasticity or there is no way to estimate it.

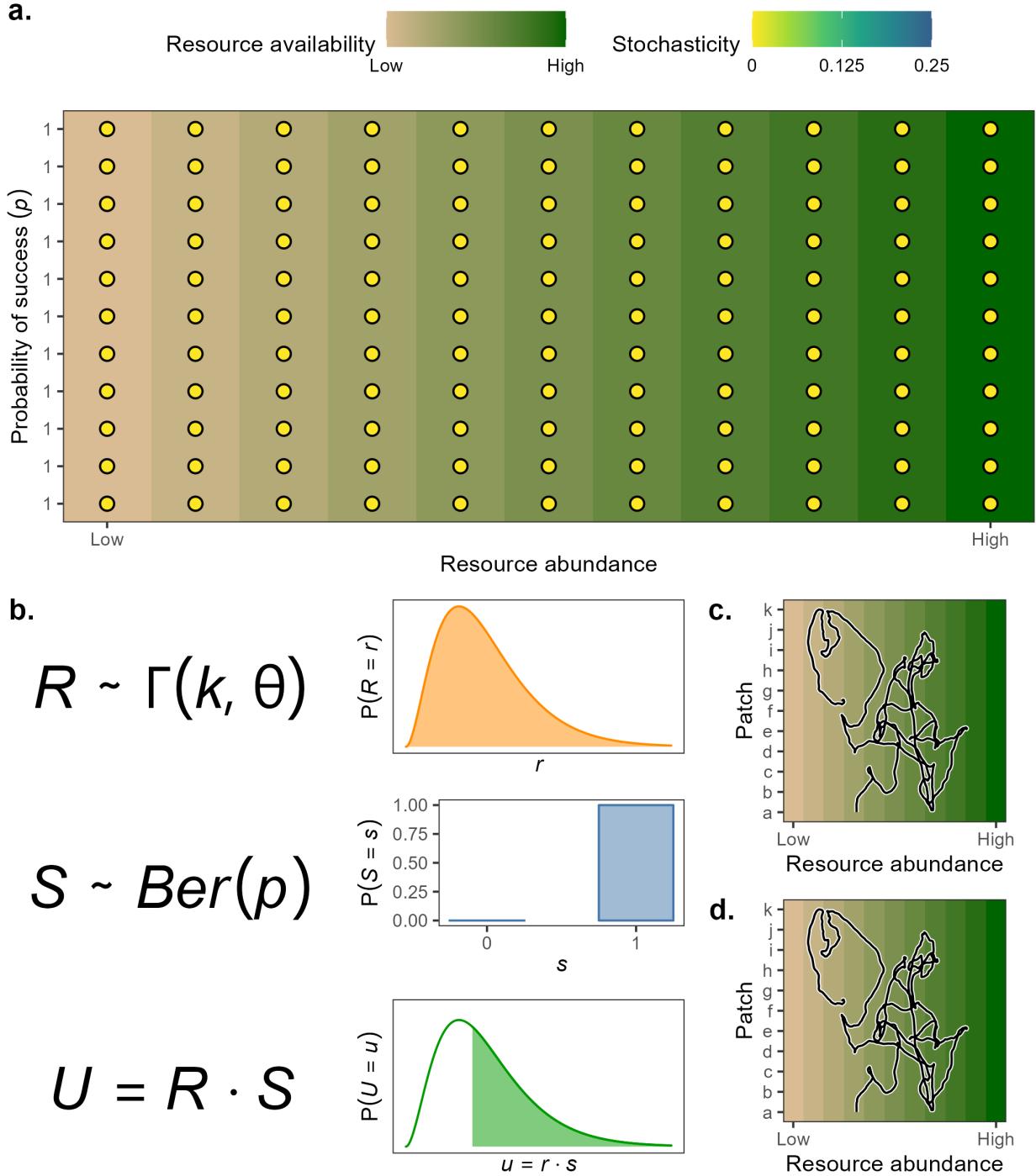


Figure 2: Fictitious example of variation in resource abundance in a heterogeneous but fully predictable environment. (a.) Complete predictability results in success (black dots) during each foraging attempt (white dots). (b.) Although the environment is heterogeneous, there is no stochasticity because it is fully predictable. (c.) Since an animal living in such an environment can expect each foraging attempt to be successful, it will likely rely more on areas with high density of resources.

In areas where animals are not guaranteed that the resources they find during one visit will be there the next time (figure 3a), stochasticity will have an appreciable effect on the location's favourableness. Patches with low or high p will be most predictable, since successes can be expected to be very rare (if $p \approx 0$) or very common (if $p \approx 1$). In contrast, patches will be most stochastic when the probabilities of success and failure are approximately the same (i.e., $p \approx 1 - p \implies p \approx 0.5$, see figure 3b). In stochastic habitats, $\mathbb{E}(U)$ will depend on $\mathbb{E}(S)$ as well as $\mathbb{E}(R)$, since S is no longer constant (figure 3c). Now, expected usable resources become $\mathbb{E}(U) = \mathbb{E}(RS)$, or $\mathbb{E}(U) = \mathbb{E}(R)\mathbb{E}(S)$ if R and S are independent. This model can be applied to all mobile animals, including herbivores, carnivores, and omnivores. In the case of herbivores, p may indicate the chance of finding good forage, which may be absent if regeneration times are long, if competitors have already exhausted the resource, or following a fire. For carnivores, p may indicate the chance of feeding on prey, which may depend on encountering and killing some first. However, since R is not limited to energetic resources, p may also indicate the chance of finding water or also a suitable location for a den or nest.

1.4 Interaction effects of resource availability and stochasticity

In the previous section, I mentioned that a model which does not account for environmental variance may be acceptable when $\sqrt{\mathbb{V}(R)}/\mathbb{E}(R)$ is low, as in the case of a habitat with high R and $p \approx 1$. However, since maximum resource abundance is constrained by environmental stochasticity (Chevin *et al.*, 2010) and resources can be depleted or rendered inaccessible by other individuals, $\mathbb{E}(R)$ does not provide a sufficiently complete picture of resource availability in an environment. Thus, the effect of $\mathbb{V}(R)$ should be included when possible, even when $p \approx 1$ or $p \approx 0$.

Let H indicate the size of an animal's HR. (We can consider specific utilization quantiles of the HR, such as the core HR ($H_{50\%}$) or the 95% HR ($H_{95\%}$), but for simplicity I will refer to the entirety of the HR with H). As explained above, H will be higher in regions with lower $\mathbb{E}(R)$ and higher $\mathbb{V}(R)$. Figure 4 presents various scenarios with different trends in $\mathbb{E}(R)$ and $\mathbb{V}(R)$

Figure 5 demonstrates how such trends can affect $\mathbb{E}(V)$ and the 95% home range estimate (which is a function of $\mathbb{E}(V)$ and $\mathbb{V}(V)$).

expand

The smoothed conditional means show 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).

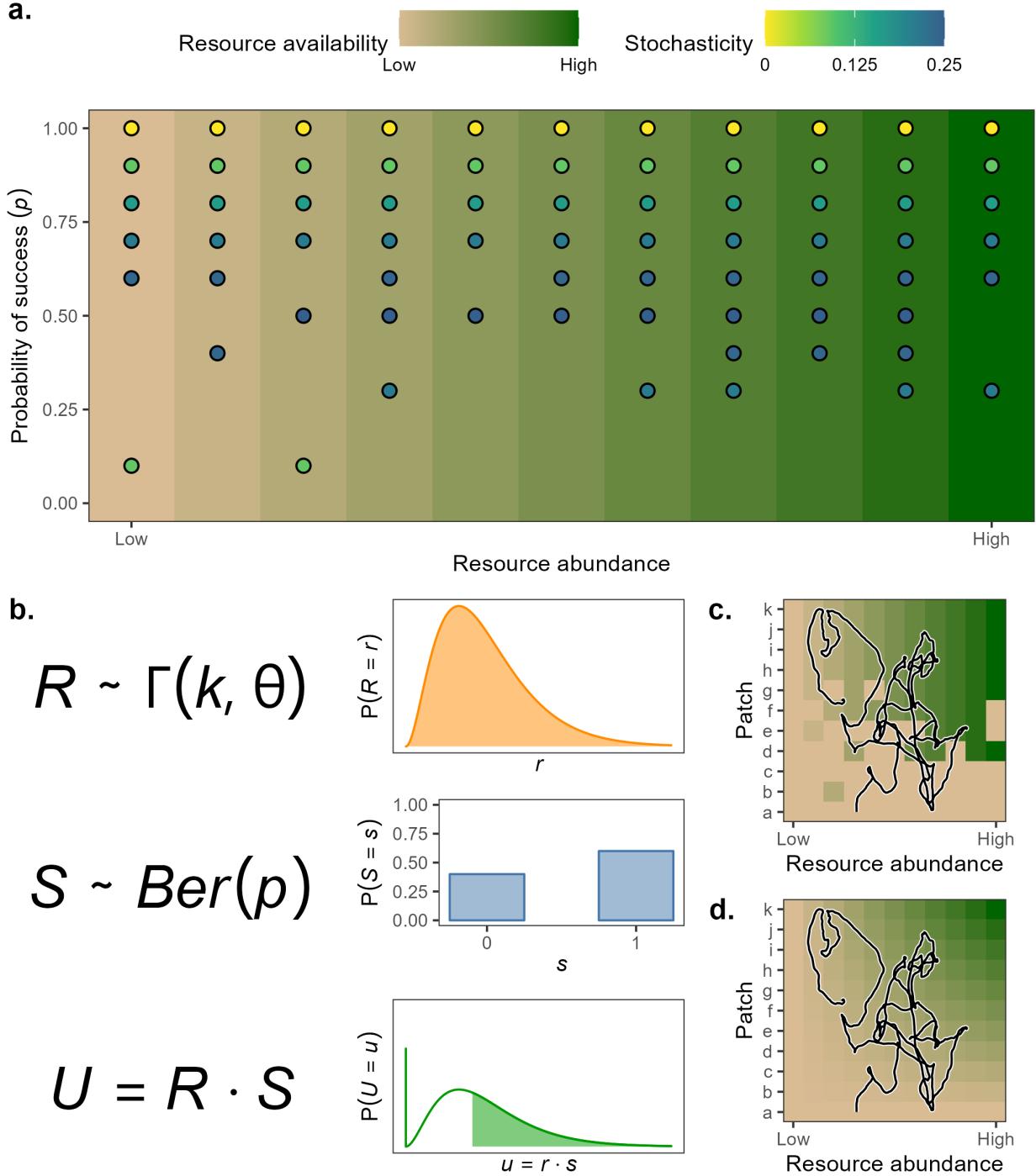


Figure 3: Fictitious example of variation in resource abundance in a heterogenous and stochastic environment. (a.) The probability of success (black dots) during a foraging attempt (white dot) can vary between patches due to various reasons, including differences in competition, predation, and resource-specific trends. (b.) Patches where the probability of success is very low (e.g., a, b) or very high (e.g., j, k) are highly predictable because animals can expect very poor or very good resource availability, respectively. In contrast, patches where the probability of success is near 0.5 (e.g., e, f, g) are highly stochastic because failure and success are approximately equally as likely. (c.) An animal living in such an environment cannot always expect each foraging attempt to be successful. When possible, animals are likely to rely mostly on predictable, resource-rich areas (top right). Alternatively, they may prefer predictable but resource-poor areas (top left) or specialize for high-risk, high-reward areas (bottom right).

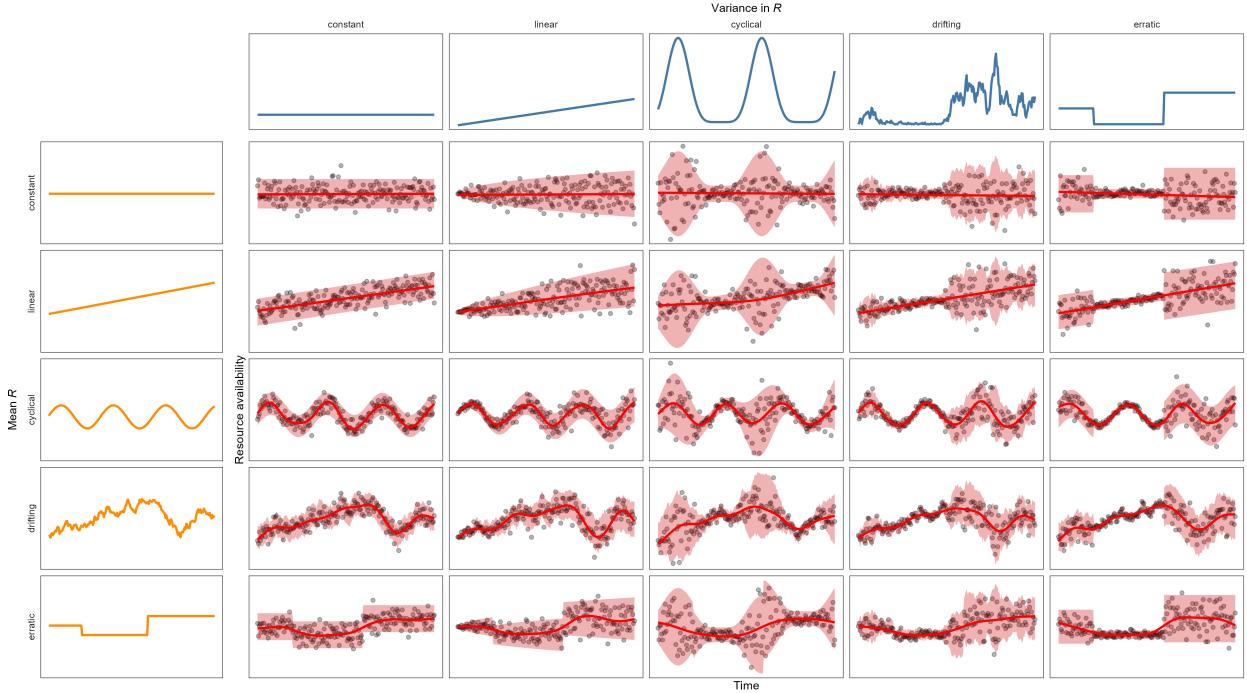


Figure 4: Simulated resource availability with constant, linearly increasing, cyclical, drifting, and erratic means or variances. The red lines are the means estimated by a Generalized Additive Model fit by the `ggplot2::geom_smooth()` function, while the shaded areas are the range of ± 2 true (i.e., not estimated) standard deviations around the estimated mean.

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.

Although some of these scenarios may seem overly simplistic

Also, a highly stochastic variance will be perceived (and 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 range shifts are required for survival,
- cyclical changes in $\mathbb{E}(R)$ and $\mathbb{V}(R)$ may occur in urban environments (Péron *et al.*, 2017) or as temperature and precipitation change between seasons (Geremia *et al.*, 2019).
- **drifting** could be because of a highly complex ecosystem with many unpredictable agents (e.g., tropical areas with high density of insects like locusts?)
- **erratic** could be because of sudden events (e.g., fires, human activity)

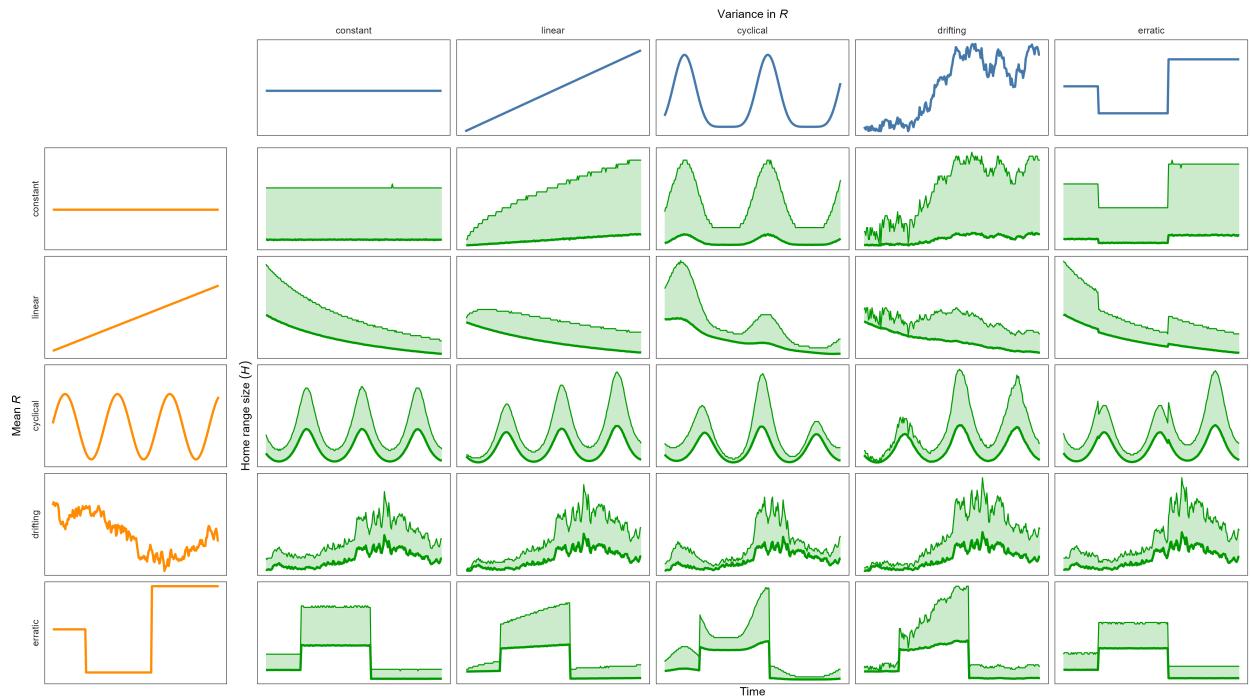


Figure 5: Simulated spatial requirements for animals living in habitats where resource availability vary with constant, linearly increasing, cyclical, drifting, or erratic means and variances. The thick line indicates the mean spatial requirement needed for survival, while the thin line indicates the 95% quantile. The thick line can also be interpreted as the animal's core home range, while thin line can be interpreted as the requirements needed for a 95% chance of survival, which would be similar to the animals' 95% home range. Changes in $\mathbb{V}(R)$ have greater impacts when $\mathbb{E}(R)$ or $\mathbb{V}(R)$ are low.

1.5 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. 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). In Chapter 2, 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.

In Chapter 3, 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.

2 Chapter 2: A new measure of environmental variance

Whether an animal is affected by or can perceive environmental variance depends strongly on the spatiotemporal scale of the process(es) involved. Processes that occur at very small scales (e.g., the location of electrons around atoms) or very large scales (e.g., the movement of the Milky Way) are unlikely to be have an effect or be detected. Thus, the scale at which we quantify variance should depend on the spatiotemporal scale and sensitivity of the animals being studied. Since this project focuses on medium to large animals, I will focus on processes and events which occur on the temporal scale of hours to decades and spatial scale of meters to kilometers. I will assume small-scale variances such as heterogeneity in grass density at the centimeter scale or fluctuations in temperature over the span of a few minutes have no (measurable) effect on the spatial needs of the animals which I will be studying. Even if such small-scale variances had an effect, such an effect would be hard to detect or quantify because: (1) the effect size would be small (so large amounts of data would be necessary for an appreciable result), and (2) the uncertainty in the tracking data limits the precision at which one is able to detect changes in movement in response to such small variation (figure 6). Thus, it seems reasonable to quantify environmental variance at the scale of minutes to days and meters to kilometers.

To my knowledge, there currently is no large-scale measurement of environmental variance. Producing a worldwide raster of such a measure would allow people to estimate the spatial temporal variance of an animal's habitat and better understand how heterogeneity and unpredictability affect its home range, as well when and why animals may decide to migrate or become nomadic. Some measures of environmental heterogeneity already exist, such as the Normalized Difference Vegetation Index [NDVI; (**ndvi-ref?**)] and the machine learning human footprint index (ml-HFI) produced by Keys, Barnes & Carter (2021). However, neither of these indices provides a comprehensive measure of environmental variance over the years. Such a measure should account for the spatiotemporal variance in frequent events (e.g., precipitation) and continuous processes (e.g., temperature) as well as the frequency of extreme and rare events (e.g., fires, cyclones).

How the frequency and average intensity of events are estimated depends on the event(s) considered. Processes for which we have an abundance of worldwide data, such as daily air temperature and precipitation can be included as raw data, and their variances can be estimated using smooth location-scale models, such as GAMs with appropriate conditional distributions (i.e., Gaussian location-scale for temperature and Gamma location-scale for precipitation; see Stasinopoulos & Rigby, 2007; Umlauf, Klein & Zeileis, 2018). In contrast, the frequency of rare events should be modeled with more smooth (i.e., less wiggly) models, since the low data availability does not allow us to use models with high degrees of freedom (i.e., very wiggly predictors;

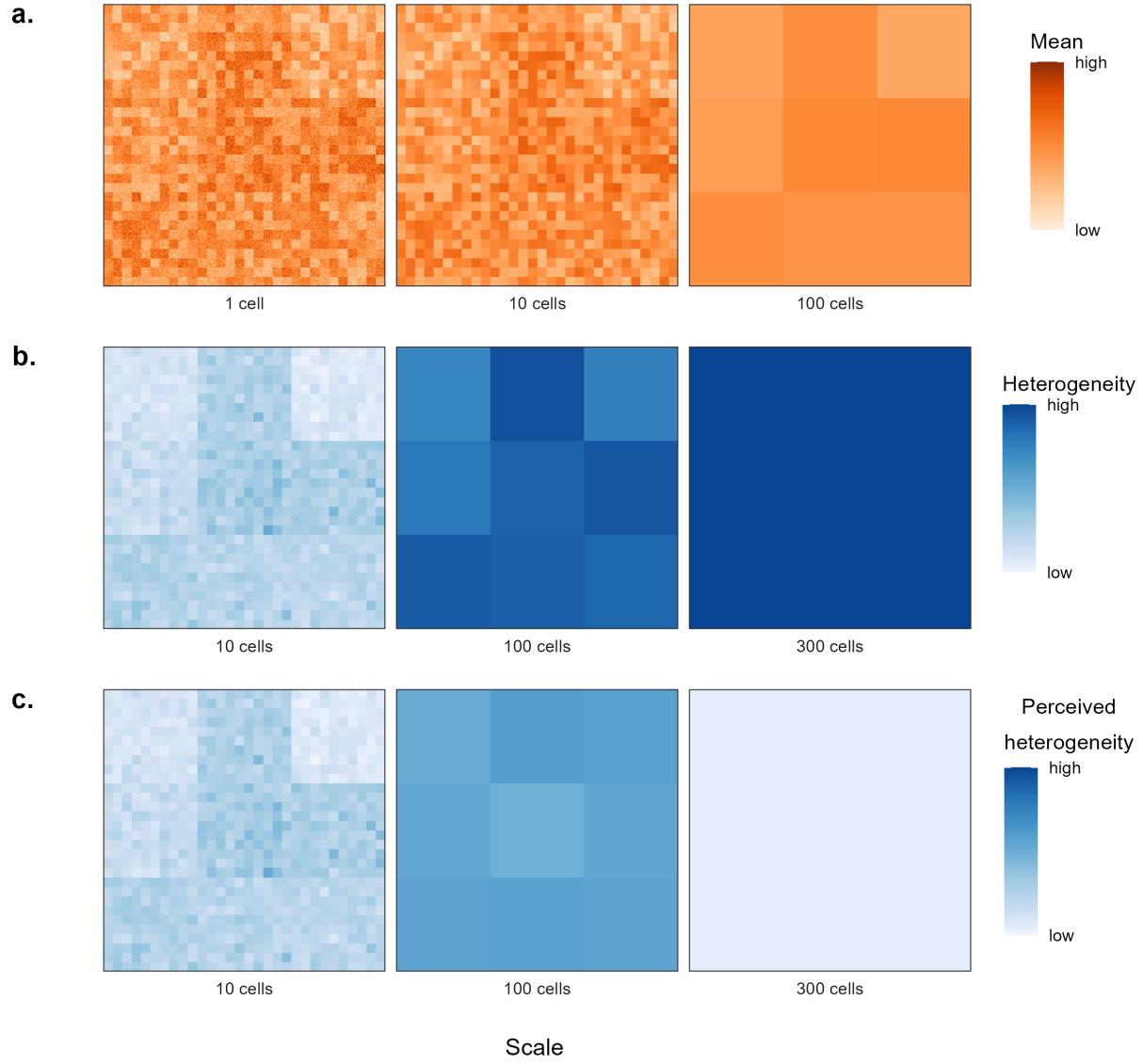


Figure 6: (a.) Fictitious means of an arbitrary random variable (e.g., resource abundance, productivity, temperature, precipitation) in a two-dimensional space. The mean value varies within small-scale patches (left), between small-scale patches (center) and large scale-patches (right). Thus, the perceived means depend on the spatial scale at which the observer can detect differences. (b.) Environmental heterogeneity detected at different degrees of precision. Wider regions have a wider range of means, which results in higher heterogeneity. Thus, each cell in the left panel represents the heterogeneity of the 100 pixels in the cell, while the cells in the central panel indicate the heterogeneity in the 10,000 cells in each of the larger cells, and the right panel indicates the heterogeneity in all 90,000 pixels. (c.) Fictitious, scale-dependent, perceived heterogeneity. The left panel is calculated as in row (b), while heterogeneity in the central and right panels are calculated on the means in the central and right panels in row (a), respectively. Perceived heterogeneity is lower than true heterogeneity because heterogeneity is lost when averaging values.

see Simpson, 2018).

The effects of environmental variance on home range size have been quantified by some small-scale studies (e.g., Lucherini & Lovari, 1996; Rizzuto *et al.*, 2021), but I was unable to find any large-scale study which estimated the effect of environmental stochasticity beyond the population or species scale.

- currently there's no raster of stochasticity
- PCA on main drivers/causes of stochasticity
- ml-HFI would be useful, but it's static
- can use NDVI, but it only starts in ~2000. however, if it correlates strongly with temperature and precip we could extrapolate out of the ranges

2.1 Environmental heterogeneity and stochasticity

There are many sources of environmental change over both time and space. Some are due to repetitive, predictable, or even well-known patterns (such as daily or seasonal changes in temperature and precipitation or the location of different patches), while others are due to infrequent, unpredictable, or poorly-understood events (such as forest fires, the arrival of new competitors, or human activity). In this thesis, I will refer to predictable or known changes in space and time as environmental *heterogeneity*, while I will use the term *stochasticity* specifically for unpredictable (spatiotemporal) variation. Examples of heterogeneity include known spatial variation between patches of variation, or expected changes in temperature throughout the day. In contrast, the spatial distribution of food in a new environment may be perceived stochastic (at least at first), since it is unpredictable. Similarly, changes in temperature ranges, precipitation, and the frequency of extreme events due to climate change (IPCC, 2018; Noonan *et al.*, 2018) are examples of stochasticity rather than temporal heterogeneity. Other unpredictable extreme events such as forest fires and floods also constitute sources of stochasticity.

Generally, events are predictable when (1) they occur with a probability density that is approximately constant over time and space, (2) they occur frequently within an organism's generation time or lifespan, and (3) they occur frequently enough to be expected as normal (e.g., rain in rainforests). (Note that the variance of a Bernoulli random variable Y is maximized when $P(Y = 1) = p = 0.5 \implies \mathbb{V}(Y) = p(1 - p) = 0.25$, and minimized when the event occurs almost never ($p \approx 0$) or almost always ($p \approx 1$), since now $\mathbb{V}(Y) \approx 0(1 - 0) = 1(1 - 1) = 0$. Thus, events which occur extremely rarely, such as meteor impacts, are predictably infrequent and often assumed not to occur.) When an event occurs fairly frequently (e.g., $0.3 < p < 0.5$), animals may begin to expect the event to occur and consider it normality (figure 3a), as long

as the change in frequency and magnitude is sufficiently gradual. For instance, Lamont *et al.* (2020) found that serotiny (the storage of seeds in closed cones or fruits which open following a fire) is common in plant populations which suffer fires at least once per lifespan, on average. However, the trait becomes less common if the fires become so common that plants survive more often as resprouters than by producing seeds. If a dangerous event such as fires becomes more frequent, unpredictable, or severe, organisms may store resources in favorable times and locations so they can resist more adverse times, and mobile animals may move to avoid such events altogether (Southwood, 1977; Lindstedt & Boyce, 1985). However, variety in fires may increase environmental heterogeneity and promote biodiversity (Fuhlendorf & Engle, 2004), particularly shortly after fires occur and when fires produce heterogeneous burns (Tingley *et al.*, 2016), but the effects of fire can differ between ecosystems (Koerner & Collins, 2013).

The timescale over which an event is (un)predictable will also play a key role in determining how species respond, or not, to stochasticity. Adverse events which occur frequently during an organism's generation time or lifespan (e.g., at least twice, on average) may be considered as threats worth preparing for. Stochastic and destructive events which happen frequently can become part of an organism's habitat and life history, so organisms may either adapt to their occurrence and even learn to predict them (Foley, Pettorelli & Foley, 2008), or they may avoid the risk altogether by moving to a new habitat (Southwood, 1977). If habitats are (or become) unfavorable, animals may move to a new habitat, migrate seasonally (Geremia *et al.*, 2019), or simply prefer nomadism over range residency (e.g., Nandintsetseg *et al.*, 2019). It is unclear when animals switch from range residency to nomadism (or vice-versa), but understanding the connection between the two types of movement is important for quantifying the effect of spatiotemporal stochasticity on animal's spatial needs. From a quantitative perspective, the switch is related to an animal's positional autocorrelation over time (also known as home range crossing time, here indicate as τ_p). Animals without a constant home range (i.e., without a constant centroid) will spend more time away from the overall mean position, so the time required to crossing their entire range time will be large.

Adverse events which are too infrequent (e.g., $p < 0.1$) may not be perceived as a reoccurring threat, so organisms may be unable to adapt appropriately. Instead, highly infrequent events are more likely to be perceived as an oddity rather than something worth preparing for. In contrast, highly stochastic events (e.g., $p \approx 0.5$ or if p changes unpredictably) may be perceived as a threat, but organisms may be unable to predict their occurrence, since it would require refined cognitive abilities. For a species or population to adapt to an event, the event must thus occur with sufficient frequency and for a sufficiently long period of time.

What an animal perceives as a stochastic process depends on the stochasticity of the process relative to the animal's size, current age (or average lifespan), and adaptability. Generally, small, short-lived, or young

organisms will tend to be more sensitive to small-scale (spatial) or short-term (temporal) changes (Southwood, 1977). 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 memory about the frequency and severity of such events (Foley *et al.*, 2008; Polansky, Kilian & Wittemyer, 2015). 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. Additionally, the effects of size and lifespan on sensitivity are likely nonlinear and correlated, since smaller animals tend to have shorter lives (and vice-versa), and small animals also tend to have lower metabolic rates, which often limit their movement speed, home ranges, and how the animals interact with their ecosystem (Brown *et al.*, 2004). Thus, processes will have stronger impacts 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 or temporal resolution. Similarly, the timing and quantity of yearly snowfall would be a somewhat 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 one animal may perceive as a single stochastic event (or cycle) may be considered as a series of short and highly stochastic events by another animal.

Figure 7 illustrates the perceived resource availability mean and variance by animals with four different levels of adaptability and how they may predict the mean and variance to change in the future (after the vertical grey line). In the extreme (and likely fictitious) case where an animal does not adapt to the environment (dark blue), it cannot react to or predict changes in mean resource abundance, and thus the perceived variance is inflated whenever the resource abundance does not match the overall mean. Environments appear highly unpredictable to such animals. Animals which can only perceive simple, linear changes in mean resource abundance (orange) perform better as long as resources continue to change linearly in the same direction (i.e. increasing or decreasing). However, they may be surprised when the trend's direction changes, as indicated by the rapid increase in variance in the top rows of figure 7b. Animals which are able to adapt smoothly (light blue) can predict changes in mean without a significant bias in estimated variance, as long as the process is not highly stochastic (unsurprisingly, see the bottom rows of figure 7). Finally, animals which adapt rapidly to changing environments may be most able to take advantage of frequent environmental changes, but they may be unable to produce reasonable predictions based on memory (*sensu* Abrahms *et al.*, 2019). Instead, they depend on constant information and only predict on the most recent

information (as indicated by the deviations from the data when predicting into the future).

While the effects of resource abundance on animal's spatial needs have been studied extensively (e.g., Lucherini & Lovari, 1996; Nilsen *et al.*, 2005; Bengsen *et al.*, 2016; Dickie *et al.* in press), the effects of environmental heterogeneity and stochasticity, including those around resource abundance, have not been given as much consideration (but see Lucherini & Lovari, 1996; Rizzuto *et al.*, 2021). 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 varies over time or space.

The recent shift to more quantitative statistical methods in environmental biology has pushed scientists to begin thinking more critically about data analysis. However, many still operate using methods and frameworks which were necessary with small datasets, but likely become problematic with an abundance of data. For instance, the widespread frequentist approach of hypothesis testing with a significance level of $\alpha = 0.05$ may often be misleading, because the significance of an effect depends on its standard error, which is a function of its sample size, since larger samples will offer a more precise and accurate measurement of the true mean. Similarly, the question of how much data is needed to detect a significant trend (Gray *et al.*, 2018) 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 the dichotomy of significance based on an arbitrary significance level. 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 (Zuur, 2009).

2.1.1 The temporal scale of stochastic events

An animal's ability to alter its behavior (including its 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 the seasons and the weather, or whether they be due to more stochastic events (e.g., natural events such as fires or floods, but also anthropogenic events like oil spills; see Matkin *et al.*, 2008), an animal's ability to adapt increases its odds of survival. Generally, temporal variation is more likely to promote plasticity over diversity, since adaptability will likely offer better odds of survival than temporally static diversity in a population or species (Bell *et al.*, 1993). 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

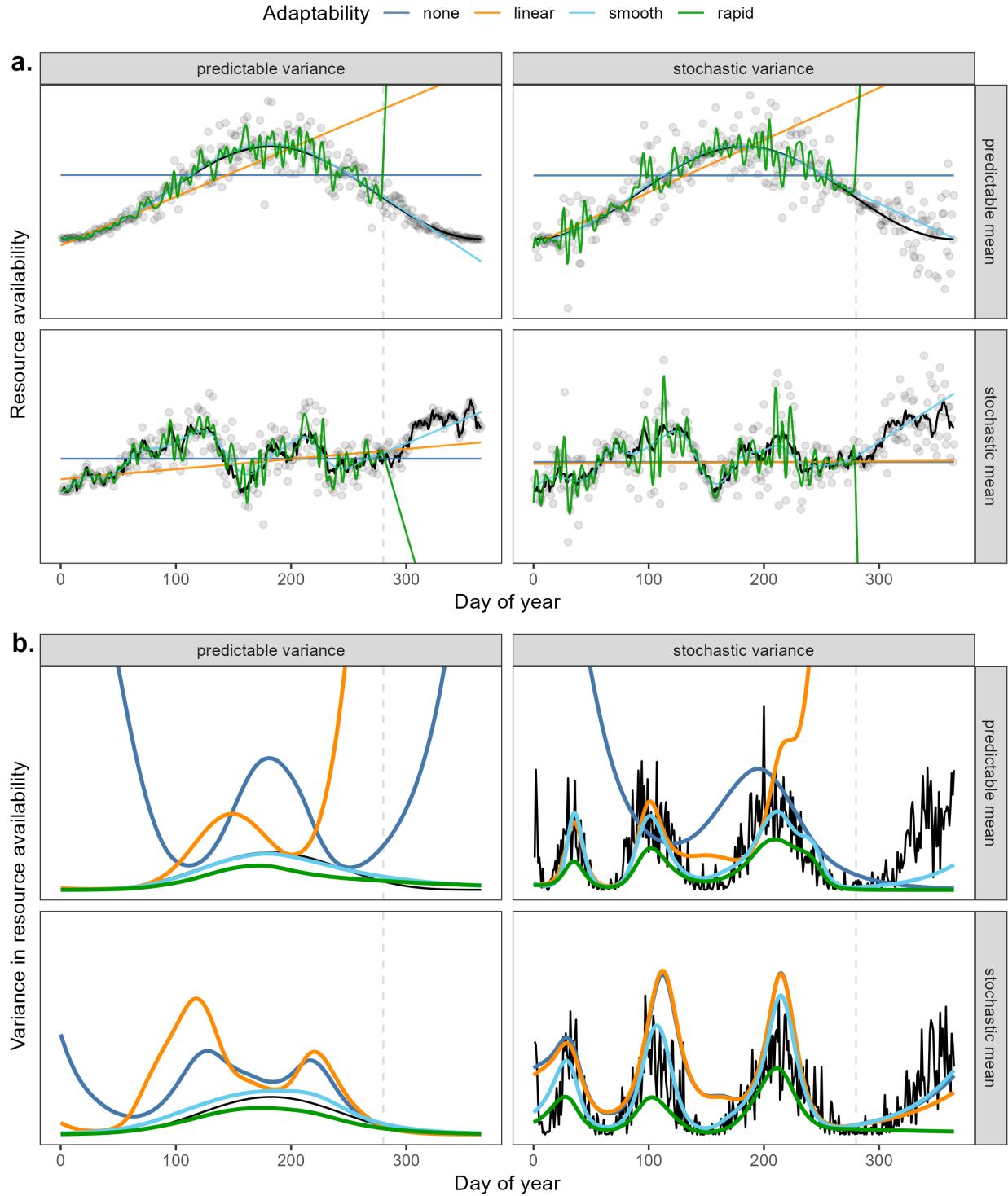


Figure 7: Fictitious changes in resource abundance mean (a) and variance (b) over the course of a year. The true trends are indicated by the black line, while the colored lines indicate the estimates perceived based on different levels of adaptability. The dashed vertical line indicates the hypothetical current date, such that any data to the right of the line is unknown to the animals, so estimates on the right of the dashed line are extrapolations. The data were simulated using Gaussian noise to ensure mean-variance independence and modeled using Generalized Additive Models with an identity link function to allow linear responses.

their migration as the climate changes, including large-scale, trans-Saharan migrants (Jonzén *et al.*, 2006). And while genetic diversity and polymorphisms also increase the odds of survival for a species (**ref?**), this project will focus strictly on animal behavior.

In an environment that changes over time, organisms which depend on mutable cycles such as changes in temperature, precipitation, and resource availability are more likely to respond to environmental changes than organisms which depend purely on 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., flying birds and large vertebrates). Although this project will focus on vertebrate animals, such changes are important to consider because the ability of a specialist or obligate symbiont to shift its home range or adapt will likely depend strongly on its associate's ability to move or adapt, too.

2.1.1.1 Temporal changes in home range The length of an animal's lifespan and the size 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 temporal and spatial scales relative to our perception of time and space. A fruit fly that lives in a building and has a lifespan of a few days is more likely to seem range-resident to us because the space it lived in is relatively small and familiar to us, but if the animal is a large mammal moving across habitats, we may tend to consider the animal a nomad. In this project, I will use a definition of home range similar to that of Burt (1943) (i.e., the area used by an animal to satisfy its essential needs) while viewing it as a continuous-time stochastic process: Since both an animal's needs and their habitat may change over time, I will consider an animal to be range resident if it inhabits a region with a stable centroid during the period of observation. While I would still consider an animal range-resident if it moved its centroid suddenly (rather than with a slow drift), the models implemented in the `ctmm` (Ctmm: Continuous-Time Movement Modeling) package for R (R Core Team, 2021) assume the centroid is stable, so I would not be able to estimate two separate home ranges. Instead, I would have to consider each region as temporary sections of the overall range. If the animal lives in a group, tracking other members of the group may help understand whether the animal shifted its home range or is not range-resident.

2.1.2 The spatial scale of stochastic events

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 litoral species. Thus, how one measures stochasticity should also depend on which organisms are of most interest.

Since species in a heterogeneous landscape can modify their behavior and move to more favorable locations, spatial variation will favor movement and behavioral adaptations faster than temporal variation will (Bell *et al.*, 1993).

Transition regions are often have the highest heterogeneity, but, similarly to temporal stochasticity, measures and perceptions of spatial heterogeneity depend on the scale at which they are being considered. 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.

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.

The same idea 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).

2.1.3 Urban landscapes and habitat structure

Human activity often fundamentally alters the structure of environments by spatially homogenizing them and imposing temporally heterogeneous and potentially stochastic cycles (e.g., mining, clear-cutting, road traffic, and weekly work schedules). The perception of spatial heterogeneity and cycles in anthropogenic areas varies between species: scavenger animals such as ravens (*Corvus corax*) and raccoons (*Procyon lotor*) often learn to recognize areas that can provide food, such as restaurants or large disposal bins, but other animals may not be able to distinguish between different urban areas. Certain animals have learned to depend on and take advantage of human activity, such as crows who place nuts strategically so that cars will crack them open for them to eat (Nihei & Higuchi, 2002).

3 Chapter 3: Movement analyses

3.1 Movement simulations

- Inform priors and simulation distributions using Indigenous Traditional Knowledge

3.2 Movement analysis

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, many commonly-used home range estimation methods (e.g., minimum convex polygon, kernel density estimation) 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 spatiotemporal autocorrelation within the data. Continuous-time models such as Ornstein-Uhlenbeck (OU) and OU foraging (OUF) models relax the assumption of spatiotemporal independence by accounting for positional autocorrelation (OU and OUF models) and directional (i.e., velocity) autocorrelation (OUF models only), which allows them to estimate the animal's average home range crossing time (OU and OUF) and the animal's average directional persistence (OUF only). Péron *et al.* (2017) provide additional information OU and OUF models and how to interpret them while also demonstrating how to use high-frequency movement data can help detect small-scale cycles, such as patterns that occur daily or weekly.

can't add HFI to analysis because it's temporally static

moving-window HR

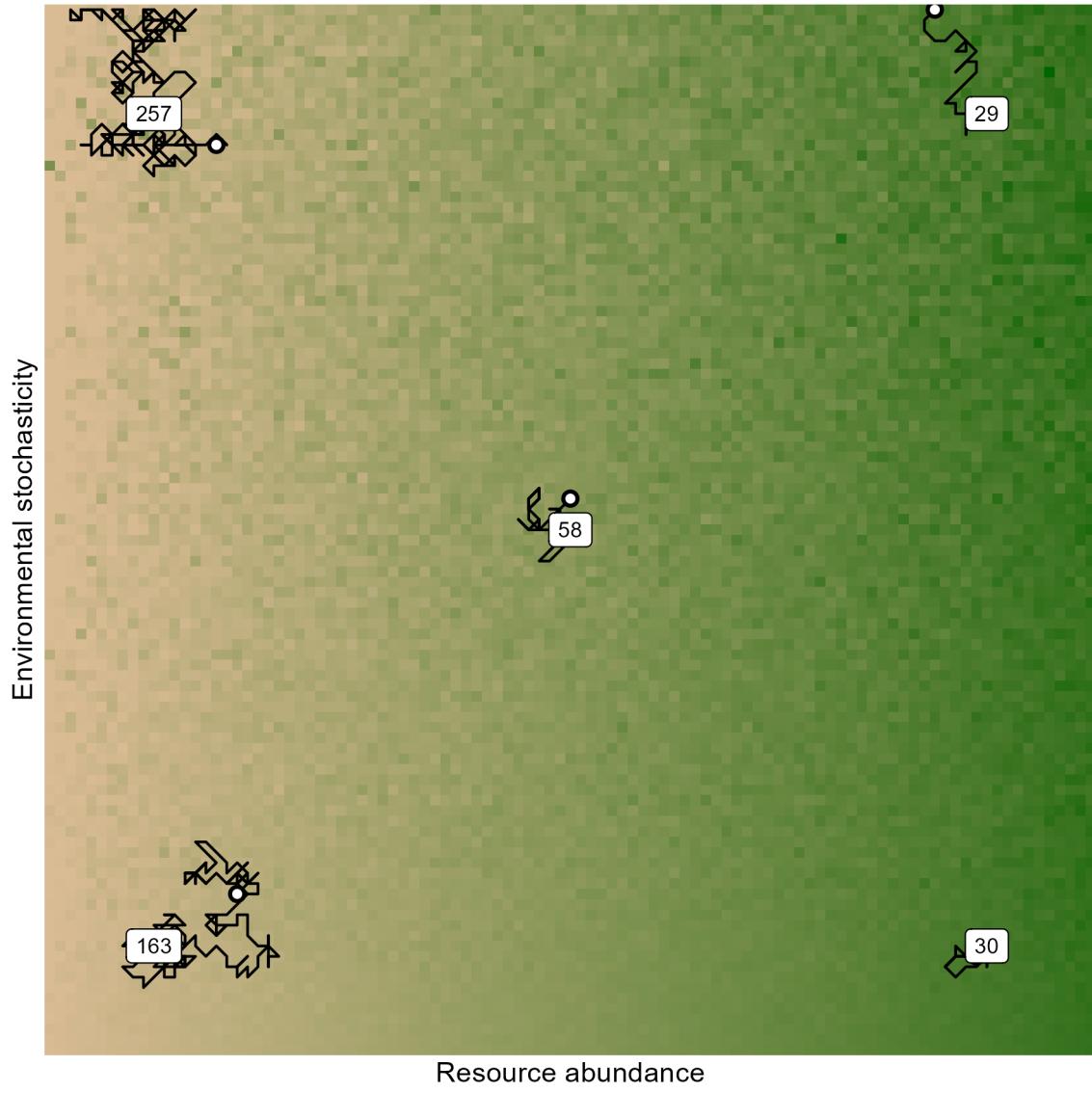


Figure 8: Simulations depicting the effects of resource availability and stochasticity on spatial needs. Animals moved from the circles to nearby tiles until sated. The labels indicate how many steps animals took to reach satiation. Note the higher spatial needs of animals in more unpredictable or resource-scarce environments. Resources were generated using a gamma random variable parameterized by independent mean and variance parameters, which represented the resource abundance and environmental stochasticity, respectively, even though the two are likely correlated in nature.

4 Chapter 4: Summary

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

From the foreword:

4.0.1 Two-eyed seeing: Recognizing Traditional Indigenous Knowledge

split into: preface, chapters 2 and 3, and conclusion; use for preface and conclusion

The lands managed and protected by Indigenous Peoples are often markedly different from those inhabited by urban societies. While recognizing that there is great diversity between Indigenous Peoples (as well as other colonized Peoples), it is important to recognize that many hold great knowledge on how to live sustainably, safeguard environments, and protect biodiversity (Schuster *et al.*, 2019), and have been doing so for millennia. Yet, their leaders and representatives are seldom included in conservation-related decision-making. Instead, many Western institutions often dismiss, ignore, and contradict the ancestral and traditional Knowledge of Indigenous and colonized Peoples (Smith, 2012). The development of Western science is frequently assumed to clash with the (often sacred) Knowledge many colonized People hold. Western science is often viewed as more objective, methodical, and unbiased than traditional Knowledge, and as such Western institutions and people often consider it 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 (ref?). 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* 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 (Bowles *et al.*, 2021). One possibility, however, is to use Traditional Knowledge to create properly informed Bayesian priors (Bolstad & Curran, 2017). The validity of the priors can be ensured using prior predictive modeling (McElreath, 2016) 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.

5 List of abbreviations used

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

6 List of notations and symbols used

Symbol	Meaning
$c \propto k$	c is proportional to k
$\mathbb{E}(\cdot)$	Expectation, mean
F	Favorableness or value of a region
H	Home range, spatial needs, required area
$P(A)$	Probability of event A , e.g., A = successful foraging
R	Resources
τ_p	Positional autocorrelation, mean reversion to HR center, range crossing time
τ_v	Velocity autocorrelation, directional persistance
$\mathbb{V}(\cdot)$	Variance

7 Project timeline

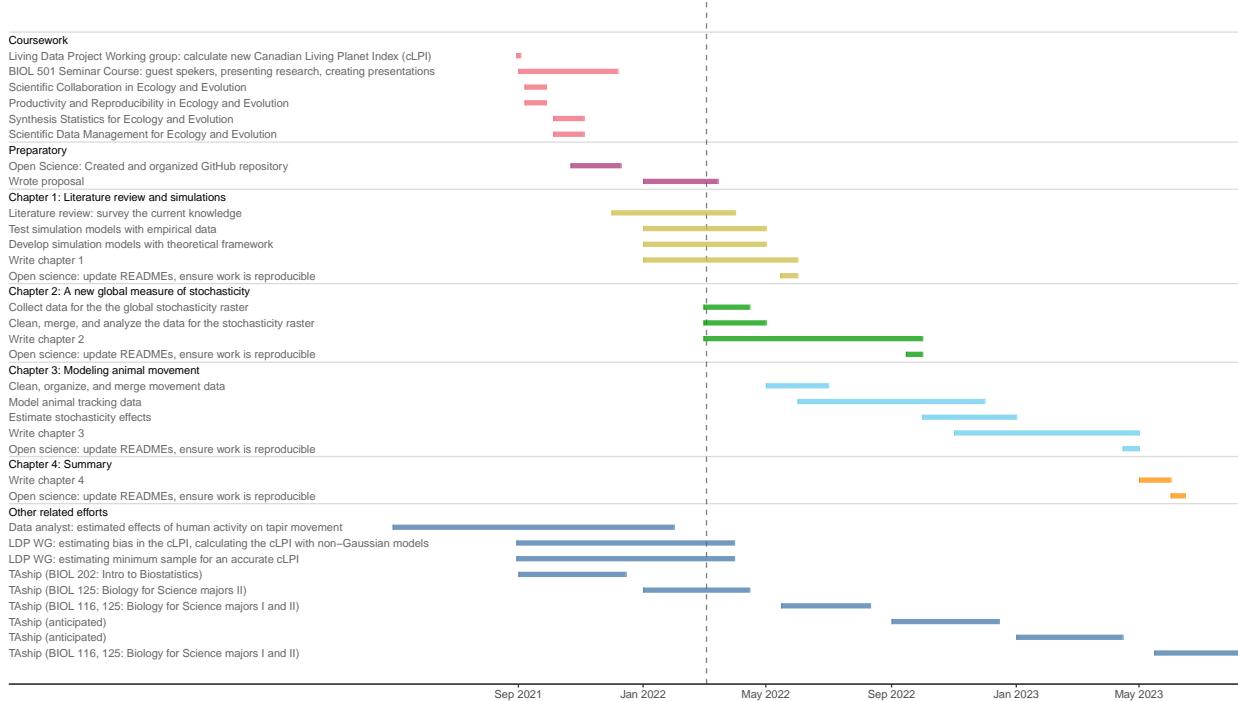


Figure 9: Visual representation of the estimated timeline for my Master's project.

7.1 Progress to date

- Created and organized the GitHub repository (<https://github.com/StefanoMezzini/hr-environ-stoch-masters>);
- Completed all coursework necessary for a Master's degree;
- Reviewed literature and have begun making theoretical predictions;
- Living Data Project Working group: calculated new Canadian Living Planet Index (cLPI);
- Data analyst: estimated effects of human activity on tapir movement using `ctmm` and `mgcv`. Code and data are available at <https://github.com/StefanoMezzini/tapirs>, while the manuscript's preprint is available at <https://www.biorxiv.org/content/10.1101/2021.11.12.468362v1>;
- Data analyst: estimated changes paleolimnological time series from endorheic lakes due to 8-m lake-level variation using Hierarchical Generalized Additive Models (HGAMs) and location-scale HGAMs fit with `mgcv`. Code and data are available at <https://github.com/simpson-lab/kenosee-white-bear>.

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Appendix 1: Manuscripts contributed to during the degree