

How resource abundance and stochasticity affect animals' spatial needs

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Abstract

Animals' spatial needs are thought to be tightly linked to the amount of resources within their habitats, such that animals living in productive habitats generally require less space than those in resource-poor habitats. Although this hypothesis has widespread empirical support, existing studies have focused primarily on responses to the mean amount of resources, while responses to the variance around the mean are still largely unknown. This is not a trivial oversight. Animals adjust to variable environmental conditions, so failing to account for the effect of resource unpredictability can result in a limited understanding of animals' spatial needs. In this study, we first review the literature of studies that estimate animals' spatial needs as a function of resource abundance. We then leverage this information to provide a unifying framework and hypotheses for the effect of mean *and* variance in resources on animals' space use. Next, we use simulated movement data to demonstrate how the combined effects of mean and variance in resource abundance interact to shape predictable patterns in animal space use. Finally, we use real-world tracking data on a lowland tapir (*Tapirus terrestris*) from the Brazilian Cerrado to show how this framework can be applied to better understand the movement ecology of free-ranging animals. Results from the simulations and empirical examples are presented using a fully transparent approach that allows researchers to apply the framework to their own data and inform area-based conservation efforts.

Introduction

The amount of resources an organism is able to access is a strong determinant of its odds of survival and reproduction. Resource limitations can cause individuals to experience a negative energetic balance, which can then result in lower fitness (Le Bot et al. 2019; Hou et al. 2020), changes to community structure (Burson et al. 2018; Ghislandi et al. 2018; Haney and Siepielski 2018; Riotte-Lambert and Matthiopoulos 2020), altered physiology (Wessling et al. 2018; Le Bot et al. 2019; Rocha et al. 2021; Dai Pra et al. 2022), lower chance of reproduction (Douglas and Pearce-Higgins 2014; Le Bot et al. 2019; Schmidt et al. 2020; Stefanescu et al. 2021), and even death (Foley et al. 2008; Berger et al. 2018). Thus, many organisms will adapt their behaviors in response to changes in local resource abundance. Some species may respond to fluctuations in resource abundance by, if possible, switching to other food sources (Le Bot et al. 2019; Steinmetz et al. 2021), and reducing energetic costs by reducing body heat (Schmidt et al. 2020) or entering hibernation or torpor (Boyles et al. 2020; Mohr et al. 2020; Fjellidal et al. 2021), but movement represents one of the most readily available traits that species can adjust, whether this be by modifying their home range (Lucherini and Lovari 1996; Relyea et al. 2000; Arechavala-Lopez et al. 2019; Bista et al. 2022; Bradsworth et al. 2022; Yu et al. 2022), migrating (Middleton et al. 2018; Geremia et al. 2019), dispersing (framework: Southwood 1977; amphibians: Cayuela et al. 2020; birds: Pretorius et al. 2020; **ref?**; mammals: **ref?**), or moving nomadically (Nandintsetseg et al. 2019; Teitelbaum and Mueller 2019).

While there are many other causes of animal movement, the relationship between animal movement and resource abundance has been of interest to biologists for over half a century. Burt (1943) considered the search for food as the primary driver for animal movement within an animal's home range. Three decades after, Southwood (1977) suggested change in resource abundance is a strong determinant of how animals decide when and where to live and reproduce. Two years later, Harestad and Bunnell (1979) proposed that the simplest relationship between resource abundance and an animal's home range size is

$$H = C/R, \tag{1}$$

where H is the animal’s **home range size**, C is the animal’s resource consumption, and R is the abundance of (usable) resources. More recently, various researches reported that home range size decreases linearly with resource abundance (desert mule deer: Relyea et al. 2000; red panda: Bista et al. 2022). Others demonstrated that spatial needs decrease nonlinearly as habitat productivity increases, with stronger decreases when resources are scarce (e.g., Canadian lynx: Herfindal et al. 2005; carnivores: Nilsen et al. 2005; tigers: Simcharoen et al. 2014; ferruginous hawks: Watson 2020). Additionally, an animal’s spatial requirements depend strongly on its metabolic rate, diet, and body weight (Harvey and Clutton-Brock 1981, 1981; Gittleman and Harvey 1982; Lindstedt et al. 1986; Reiss 1988; Boratyński 2020; Noonan et al. 2020). Thus, there are many drivers of animal movement and many causes of variety between behaviors, and we currently lack a unifying framework for quantifying the effects of resource abundance and unpredictability on animals’ spatial needs. And while abundant work has been done on estimating animals’ responses to changes in resource abundance, there is little to no information on they respond to unpredictable changes in the resources they depend on.

In this paper, we refer to a location’s average amount of available and accessible resources as **resource abundance**, while use the phrase **resource unpredictability** to indicate the variability in resource abundance due to *unpredictable* causes. On its own, a habitat’s long-term resource abundance is not sufficient to assess the habitat’s quality. A grassland with relatively low but constant forage availability will require drastically different behaviors and adaptations from a desert location with rare, sudden, and strong pulses of resources. In the first scenario, an animal may require a large but constant home range as it moves between locations in search of food, while an animal in the second scenario may switch between dispersal as it searches for high-resource patches and short-term range residency until the local resources are exhausted. Although both habitats may have the same long-term average

resource abundance, the differences in resource unpredictability result in substantially different habitats. Despite this, little work has been done on estimating the effects of resource unpredictability on animals' spatial needs (Herfindal et al. 2005; Nilsen et al. 2005; but see Rizzuto et al. 2021).

In this study, we illustrate how animals' spatial needs depend on the abundance and unpredictability of resources. First, we set the theoretical background necessary for the successive sections, and concepts and notation are introduced without assuming any previous knowledge of statistical notation or movement ecology. Next, we provide a review of the effects of resource abundance on animals spatial needs while suggesting a unifying hypothesis. Afterwards, we provide a review of the effects of resource unpredictability on animals spatial needs while suggesting a second unifying hypothesis. Subsequently, we test the two hypotheses using quantitative simulated animal responses to changes in resource abundance and unpredictability. Finally, we demonstrate how this framework can be used in practice to describe the movement ecology of a lowland tapir living in the Brazilian Cerrado. Results from the simulations and empirical example are presented using a fully transparent approach that allows researchers to replicate the work and apply the methods to their own tracking data.

Concepts and definitions

Resources as a random variable

In statistics, **random variables** indicate random (i.e., unknown) quantities and are indicated with capital letters (e.g., R). Known values, such as realizations of random variables (i.e., known observations or instances), are indicated with lower-case letters (e.g., r). Using this notation, we can write the statement “the probability of random variable R taking the value r ” as $P(R = r)$. Since resource abundance depends on a variety of factors, including climate, weather, competitive pressure, and individual- and species-specific energetics, it is often unpredictable (and hard to quantify). Thus, we can let the random variable R indicate the *resource* abundance at a given point in space and time.

Probability distributions

In probability and statistics, random variables are defined by specifying the **distribution** the variable follows. Since the variable is random, it can take multiple values (minimum 2), each with different probabilities. Commonly known distributions include the normal (i.e., Gaussian) distribution, the Student’s T distribution, and the Bernoulli distribution.

The set or range of values which have non-zero probabilities in a distribution are referred to as the distribution’s **support**. The support of the normal and T distributions are all real numbers (i.e., from $-\infty$ to ∞), while the Bernoulli distribution only has support over values 0 and 1.

There are many distributions we can assign to R , depending on how we quantify it. If R is the number of calories an animal is able to access from food in a given location, we can let R follow any distribution with support over all real numbers between 0 and infinity, which we can indicate with $r \in (0, \infty)$. (We use round parentheses rather than square brackets (i.e., $[0, \infty]$) because both 0 and infinity are not included in the support set.) In this case, we can let R follow a Gamma distribution. If R was a discrete variable, such as the number of prey

in a location during a period of time, we can use a Poisson or negative binomial distribution for R . Alternatively, if we measure R using the Normalized Difference Vegetation Index (NDVI, see Pettorelli et al. 2011), we should use a distribution with support over the interval $[-1, 1]$, since NDVI can only take on values between -1 and 1 (extremes included). The next two sections introduce two parameters that are often used to visualize and define distributions: the expectation and the variance of a random variable.

Expected resource abundance, $\mathbb{E}(R)$

The **expectation** of a random variable (i.e. its mean or average, indicated here with the symbol \mathbb{E}) is the value one can *expect* the random variable to take. $\mathbb{E}(R) = \mu$ to indicate the expectation of the random variable R . The mean may not be within the distribution's support (e.g., a non-integer number of prey per day), but $\mathbb{E}(R)$ is still useful for estimating the average long-term resource abundance. When the mean changes over time, as in the case changes in R in highly seasonal regions, we explicitly indicate that $\mathbb{E}(R) = \mu$ changes over time by writing the expectation of R as a function of time, t : $\mathbb{E}(R) = \mu(t)$. We indicate the estimated average resource abundance by adding a caret on the symbol: $\hat{\mu}(t)$.

The hypothesis that spatial needs decrease with resource abundance is common and well supported, but many studies assume a linear relationship (e.g., Harestad and Bunnell 1979; Relyea et al. 2000; McClintic et al. 2014; Rizzuto et al. 2021; Bista et al. 2022; Bradsworth et al. 2022). This is problematic because it can lead to questionable estimates and problematic biases, such as negative or excessively small home ranges (e.g., figure 2 in the work of Bista et al. 2022). Conceptually, the relationship between spatial needs and resource abundance must be nonlinear, since there are limits to how much space an animal is able to explore in its lifetime and the minimum amount of space it requires to survive (which is necessarily greater than zero). The relationship between resource abundance and animals' spatial needs is explored in more depth in a following section.

Variance in resource abundance, $\mathbb{V}(R)$

A random variable's **variance** is a measure of its unpredictability or variability. We use $\mathbb{V}(R) = \sigma^2$ to indicate the variance in R , after accounting for changes in $\mu(t)$, and $\widehat{\sigma^2}(t)$ to indicate its estimate conditional on time. For instance, while one may consider R to vary within years, we define $\mathbb{V}(R)$ as the variation in R after accounting for the fact that R is lower during some seasons and higher in others. Additionally, we distinguish between two different sources of variation. We refer to known differences or expected spatiotemporal changes as **heterogeneity**, while we use the term **stochasticity** for unpredictable and unexpected variation. For example, the location of (high-yield) berry bushes in a valley and the time at which they produce fruit may be heterogeneous, but predictable once an animal visits the valley. In contrast, whether next year will be a good or bad year for berries is stochastic.

Simulating resource abundance

In this paper, we simulate R using a Gamma distribution with time-dependent mean $\mu(t)$ and time-dependent variance $\sigma^2(t)$ (which we write as $R \sim \Gamma(\mu(t), \sigma^2(t))$). Although Gamma distributions are more often parameterized using parameters shape and scale (k, θ) or shape and rate $(\alpha, \beta = 1/\theta)$, we use $\mu = k\theta$ and $\sigma^2 = k\theta^2$ to facilitate visualizing the examples. However, note that μ and σ^2 are not independent because the variance depends strongly on the mean. As the mean approaches zero (from the positive side, which we write as $\mu \rightarrow 0^+$) the variance also does: $\mu \rightarrow 0^+ \iff k\theta \rightarrow 0^+ \iff k\theta^2 = 0^+ \iff \sigma^2 = 0^+$.

Estimating resource abundance using NDVI

In this paper's empirical example, we estimate resource abundance using NDVI (for more information, see the relevant section later in the paper and Pettorelli et al. 2011). However, since there is no commonly used distribution with a support over the interval $[-1, 1]$ we scale NDVI to the interval $[0, 1]$ to use a Beta distribution by applying the linear transformation

$$R = \frac{\nu + 1}{2}, \quad (2)$$

where ν indicates the NDVI value. Note that only **linear transformations** (i.e. only addition, subtraction, multiplication, and division) should be applied to random variables to avoid biases while estimating the distribution and its parameters (Jensen 1906; Denny 2017). In this case, we can define R as following a Beta distribution with mean and variance that depend on time using the notation $B(\mu(t), \sigma^2(t))$. We use this parameterization here for ease of explanation, but note that Beta distributions are generally parameterized using the shape parameters α and β such that the mean is

$$\mu = \frac{\alpha}{\alpha + \beta} \quad (3)$$

while the variance is

$$\sigma^2 = \frac{\alpha\beta}{(\alpha + \beta)^2(\alpha + \beta + 1)}. \quad (4)$$

Failing to model or simulate resource abundance appropriately can fail to produce robust, sensible, and accurate results.

Animal movement as a stochastic process

Drivers of animal movement

Nathan et al. (2008) generalized animal movement from location \vec{l}_t to location \vec{l}_{t+1} using the model

$$\vec{l}_{t+1} = F(\Omega, \Phi, \vec{w}_t, \vec{l}_t, \vec{\xi}_t), \quad (5)$$

such that an animal's position as time $t + 1$ depends on its motion capacity (Ω), navigation capacity (Φ), internal state (\vec{w}_t) and current location (\vec{l}_t), as well as how each of the

parameters may change in response to the current environmental factors ($\vec{\xi}_t$). This model is conceptually useful, as it can form the basis for many models, experiments, and hypotheses, but fitting such a model would be very difficult in practice (if not impossible). The parameters Ω , Φ , \vec{w}_t and $\vec{\xi}_t$ cannot be quantified directly, and although it may be possible to monitor proxies for the parameters (e.g., body size, memory, cortisol levels), doing so with sufficient frequency and accuracy would not be simple. Thus, we can instead focus on animals' behavior and spatial needs as a response to overall resource abundance and unpredictability.

Visualizing movement as a stochastic process

To understand how movement can be viewed as a **stochastic process**, imagine an animal that leaves its den or nest to collect resources and returns to it once it has collected enough resources for the day. If we do not know why the animal is choosing to move in one direction or another, nor do we know what the environment is like, we cannot predict where the animal may move from one time point to another. However, we can use the animal's positional data to estimate the amount of time it spends collecting resources before returning "home" (or the time required for the position to "decay" back to the average position). This period is often referred to as the **range crossing time** or the positional autocorrelation parameter, τ_p . Similarly, we can define τ_v to be amount of time the animal moves with the same direction and speed, or the time required for an animal's velocity to "decay" back to the average velocity. τ_v is referred to the animal's **directional persistence** or the velocity autocorrelation parameter.

By modeling movement via stochastic models which account for autocorrelation in position (e.g., Ornstein–Uhlenbeck or OU models, see Uhlenbeck and Ornstein 1930) and autocorrelation in velocity (Ornstein–Uhlenbeck Foraging or OUF models, see Fleming et al. 2014), one is able to account for and leverage autocorrelation in tracking data. While autocorrelation is problematic for models that assume locations to be independent, modeling

movement as a stochastic, autocorrelated process avoids systematic biases in the estimation of home ranges (Noonan et al. 2019b) as well as travelling distances and speeds (Noonan et al. 2019a).

Accurate speed estimates require the **sampling interval**, Δt , to be sufficiently small ($\Delta t < \tau_v$, see Noonan et al. 2019a), since the dataset must contain multiple consecutive samples where the animal is moving with a similar speed and direction. However, since the time required for an animal to cross the area it uses is orders of magnitude larger than the time it moves with a consistent behavior (i.e., $\tau_p > \tau_v$), it is still possible to produce good estimates of range crossing time even if there is no information on the animal’s speed. Similarly, if the data is too sparse to estimate τ_p , one can still obtain good estimates of the animal’s spatial needs and home range size, provided that the total **sampling duration**, T , is sufficiently long. Model selection procedures with criteria such as AIC (Akaike 1974) can help choose the most appropriate model for the available data (Silva et al. 2022).

Predicting animal movement using stochastic models may seem less straightforward and more complex than using deterministic models, but ignoring the exact causes and decisions that determine the movement allows us to focus on *how* the animal moved and less *why* it moved. Animals may temporarily change their behavior in response to many causes, including predators (mule deer: Ciuti et al. 2012; shovelnose sturgeon: Hintz et al. 2013; rodents: Randler and Kalb 2020; macaques: Liu et al. 2022; but also see beaked whales: Siegal et al. 2022), competitors (Capuchin monkeys: Tórrez-Herrera et al. 2020), weather (framework: Gibert et al. 2016; giant anteaters: Giroux et al. 2022), and mates or mating periods (feral cats: Zhang et al. 2022; yellow mongoose: Cronk and Pillay 2021).

Quantifying spatial needs

The concept of a home range has a long history in ecological research as an indicator of the space an animal requires to satisfy its essential requirements during a period of time (Burt 1943), but home range analysis is not appropriate for animals which are not range-resident,

such as migrating animals (e.g., Jonzén et al. 2006; Abrahms et al. 2019; Geremia et al. 2019) and nomadic animals (e.g., Morato et al. 2016; Nandintsetseg et al. 2019). Although here we quantify animal’s spatial needs using 50% and 95% home range estimates, we expect that similar conclusions can be drawn about the positional variance, $\mathbb{V}(\text{position})$, of animals that are not range-resident. In the case of animals that are range resident for short periods of time, we can model their movement and short-term spatial needs using a sliding window approach (see the discussion section).

I don’t think we need this paragraph: Although range-resident animals will generally have smaller positional variance ($\mathbb{V}(\text{position})$) than migratory and nomadic animals, $\mathbb{V}(\text{position})$ is not sufficient to distinguish between range residency, migration, and nomadism, since $\mathbb{V}(\text{position})$ determines the scale and size of an animal’s spatial needs but not its behavior. Instead, the animal’s τ_p , τ_v , and \bar{v} can help discriminate between different behaviors. Animals with a τ_p shorter than a year are likely range-resident, while animals with a τ_p on the order of a year are likely to be migratory (as long as their life expectancy is greater than a year). In contrast, when an animal’s τ_p is on the order of its expected lifespan, it is most often nomadic, since it does not have a position it returns to regularly.

Effects of resource abundance, $\mathbb{E}(R)$

While animals' needs vary greatly between taxonomic groups, some needs are essential for most species for survival and reproduction. All heterotrophic organisms require sources of chemical energy (i.e., food), water, and various limiting nutrients to survive, grow, and reproduce (Harvey and Clutton-Brock 1981; Baldwin and Bywater 1984; Reich 2001). Failing to acquire sufficient resources is likely to result in lower fitness, behavioral changes, physiological changes or damage, inability to reproduce, and death. Motile organisms can move to new locations in search of resources, but they must also account for a higher metabolism and movement costs (Taylor et al. 1982).

The size of an animal's spatial needs is often hypothesized to depend on resource abundance (Burt 1943), such that spatial needs increase when resources are low, but the relationship is likely not linear, as illustrated in figure 1 (Herfindal et al. 2005; also see: Nilsen et al. 2005; Bista et al. 2022). Low values of $\mathbb{E}(R)$ force animals to have larger home ranges (Relyea et al. 2000; Herfindal et al. 2005; Nilsen et al. 2005; Bista et al. 2022), migrate to better locations (Samarra et al. 2017; Middleton et al. 2018; Geremia et al. 2019), or move nomadically (Singh et al. 2012; Polansky et al. 2015; Nandintsetseg et al. 2019; Teitelbaum and Mueller 2019), although large-scale changes in behavior (such as species-wide shifts to dispersal, migration, or nomadism) are more likely to occur over evolutionary timescales rather than an animal's lifespan.

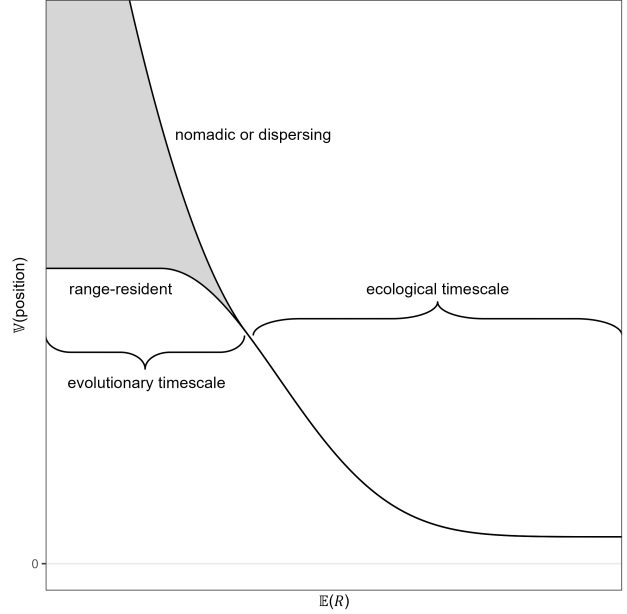


Figure 1: Hypothesized spatial needs (indicated as positional variance, $\mathbb{V}(\text{position})$) of an animal as a function of mean resource abundance ($\mathbb{E}(R)$). We expect low values of $\mathbb{E}(R)$ to result in high $\mathbb{V}(\text{position})$ as animals are forced to explore greater areas to collect the resources they require to survive, whether they be range-resident or nomadic. As $\mathbb{E}(R)$ increases, spatial needs should decrease nonlinearly until they reach the minimum amount of space required by the animal to survive. Note that the relationship between $\mathbb{E}(R)$ and $\mathbb{V}(\text{position})$ cannot be linear because it would require $\mathbb{V}(\text{position})$ to be negative for high values of $\mathbb{E}(R)$.

As $\mathbb{E}(R)$ increases, we expect animals' spatial requirements to decrease nonlinearly until they reach the smallest amount of space required to survive (see Relyea et al. 2000; Bista et al. 2022, although the latter uses models which assume linear relationships). The spatial requirements initially decrease rapidly since small additive increases (e.g., from 1 to 2) are proportionally large (i.e., 2 is twice 1). In contrast, at higher values of $\mathbb{E}(R)$, the same additive changes (e.g. from 50 to 51) are proportionally small (i.e., 51 is only 2% larger than 50).

Animals living in large groups will often require larger home ranges because they will have to share resources with conspecifics (Prox and Farine 2020), and larger home ranges can be harder to defend and also result in higher rates of competition and movement costs (Grant 1993; Jetz et al. 2004; but also see Dickie et al. 2022). While competition may push animals to explore other areas and expand their home range (Jetz et al. 2004), strong and consistent competition paired with territorial defense may also prevent them from doing so (wolves: Rich et al. 2012; feral cats: Bengsen et al. 2016; Capuchin monkeys: Tórrez-Herrera et al. 2020).

It is unclear when animals switch from range residency to migration or nomadism (or vice-versa), but understanding the connection between the types of movement is important for quantifying the effect of resource abundance on animal's spatial needs and when an animal may choose to migrate or disperse rather than remaining range-resident (mammals: Teitelbaum et al. 2015; moose: Singh et al. 2012; eagles: Wheat et al. 2017; Poessel et al. 2022; flamingos: Pretorius et al. 2020). From a quantitative perspective, the switch is related to an animal's home range crossing time (or positional autocorrelation, τ_p). As the amount of space an animal uses over its lifespan, the amount of time required to cross the area (τ_p) will also increase, so animals with τ_p on the order of their expected lifespan will necessarily be nomadic.

Consider the simplistic scenario where the average in resource abundance, $\mathbb{E}(R) = \mu$, changes over time but $\mathbb{V}(R) = \sigma^2$ is constant over time and space (and non-zero, see figure

2a). We can use the notation $R \sim \Gamma(\mu(t), \sigma^2)$ to indicate that R follows a Gamma distribution with a mean $\mu(t)$ that changes over time (i.e., it is a function of time) while the variance is constant (figure 2b). Since R is spatiotemporally random, an animal that moves in the landscape will not find the same R at different time points or throughout the habitat (figures 2c-d). However, if $\mu(t)$ changes repetitively and regularly over time (e.g. peaks each spring and decreases in winter), an animal may learn to predict times of high or low R (Samarra et al. 2017; Abrahms et al. 2019, 2019; Geremia et al. 2019; e.g., Falc3n-Cort3s et al. 2021) although it will not be possible to predict where high- R locations are, since $\mathbb{E}(R)$ does not vary predictably over space.

This model is somewhat simplistic, but its simplicity makes it easy to fit and conceptualize. Such a model may be appropriate in regions with little to no changes in variability and where unpredictable events occur at a similar frequency over time, or when data availability is too low to produce appreciable measures of variance. Examples of temporally homogeneous habitats include regions where productivity remains fairly predictable throughout the year (e.g., equatorial rain forests or highly homogeneous deserts). When productivity is approximately stable over long periods of time, it may be possible to further simplify the model by assuming a constant mean, but this is likely rarely the case. Most often, $\mathbb{E}(R)$ will vary over time, and animals' behaviors will change in response. Additionally, when data availability is sufficiently high to produce

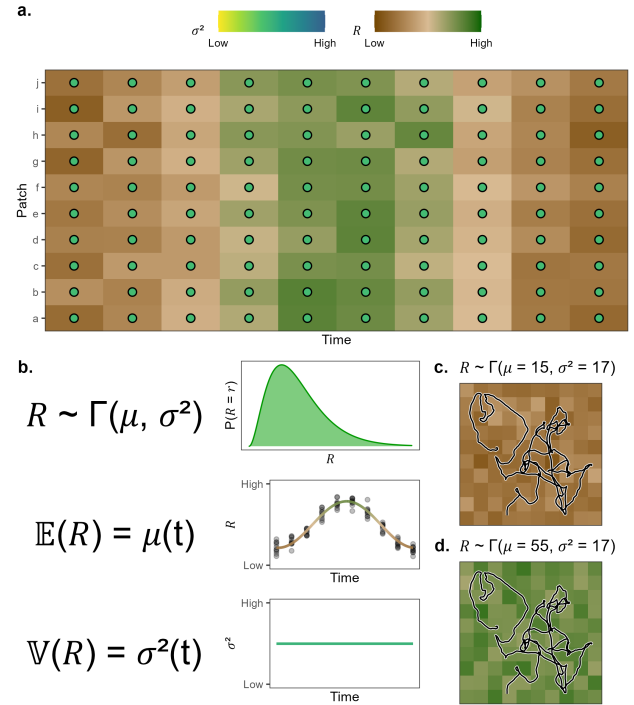


Figure 2: Fictitious example of variation in resource abundance in a heterogeneous environment with constant variance (after accounting for changes in mean abundance). (a.) Although resource abundance (R , raster fill) varies over time and space, the overall amount of variance (dot color) remains constant. (b.) Arbitrary definition of R as following a Gamma distribution with mean μ and variance σ^2 . (c.) Simulated animal movement at a time of lowest $\mathbb{E}(R)$ and average $\mathbb{V}(R)$. (d.) Simulated animal movement at a time of peak $\mathbb{E}(R)$ and average $\mathbb{V}(R)$.

precise estimates of $\mathbb{V}(R)$, the effect of $\mathbb{V}(R)$ on animals' spatial needs should be estimated before assuming the effect is negligible. The need to account for $\mathbb{V}(R)$ is compounded by recent changes in climate, which exposes species to novel situations and increasingly common stochastic events (IPCC 2018; Noonan et al. 2018).

Anthropogenic changes, including human-built structures and urban areas reduce the habitat available to many terrestrial species (Wilson et al. 2016), who struggle to move in fragmented (Fahrig 2007), human-dominated landscapes (Tucker et al. 2018). Although some species rely on anthropogenic areas and structures for predictable and dependable sources of resources (wild boar: Ikeda et al. 2022; elephants: Benitez et al. 2022; steppe rat snake: Yu et al. 2022; yellow mongoose: Cronk and Pillay 2021; common octopus: Arechavala-Lopez et al. 2019; raccoon dog: Mitsuhashi et al. 2018; coyote: Péron et al. 2017), anthropogenic environments can be highly unpredictable and pose high mortality risks (giant anteaters: Noonan et al. 2021; killer whales: Matkin et al. 2008). Although it is generally acknowledged that animals will modify their behavior in response to human activity (Rogala et al. 2011) as well as changing conditions (Walther et al. 2002; Chevin et al. 2010; Sih et al. 2011), a fine-scale understanding of behavioral responses is lacking (Sih et al. 2011; Beever et al. 2017).

Effects of resource unpredictability, $\mathbb{V}(R)$

Although the effect of R on animals' spatial needs is often recognized and accounted for in ecology (Burt 1943; Southwood 1977; Relyea et al. 2000; Nilsen et al. 2005; Williams-Guillen et al. 2006; Rickbeil et al. 2019), $\mathbb{V}(R)$ has received far less attention (but see Lucherini and Lovari 1996; Nilsen et al. 2005; Di Stefano et al. 2011; Rizzuto et al. 2021; Seigle-Ferrand et al. 2021). However, $\mathbb{V}(R)$ can change strongly due to many important causes, including repetitive and predictable patterns as well as infrequent and unpredictable events. Examples of predictable changes in $\mathbb{V}(R)$ include changes that occur between seasons, such as changes

in temperature in continental summers (e.g., between 15 and 30 °C) and winter temperatures (e.g., from -40 to -10°C within the span of a few days), changes in precipitation frequency and unpredictability between the dry season (predictable lack of rain) and the wet season (frequent but sudden and unpredictable rains), or changes in fruit and berry abundance with the arrival of spring and summer (since the timing between plants can depend on many unaccounted factors). Although each of these events is unpredictable, the change in unpredictability can be predicted and expected. In contrast, other sources of stochasticity can be much less predictable, such as new competitors (ref?), fires (Jolly et al. 2022), floods (Ramos Pereira et al. 2013), droughts (Foley et al. 2008; Haig et al. 2013), and changes in climate (Grant et al. 2017; Berger et al. 2018; IPCC 2018; Noonan et al. 2018; Yao et al. 2022).

Environmental variability, including extreme events (Logares and Nuñez 2012; Anderson et al. 2017; Yao et al. 2022), can reduce a landscape’s energetic balance (Chevin et al. 2010), which, in turn, decreases animals’ fitness (Berger et al. 2018) and increases their spatial needs. A few recent studies support this hypothesis (Morellet et al. 2013; Nandintsetseg et al. 2019; Riotte-Lambert and Matthiopoulos 2020), but many of them are limited in geographic and taxonomic scales, so the extent to which these preliminary findings can be generalized is still very limited. Thus, there remains a need for developing a more complete understanding of how animals’ spatial needs change with environmental stochasticity.

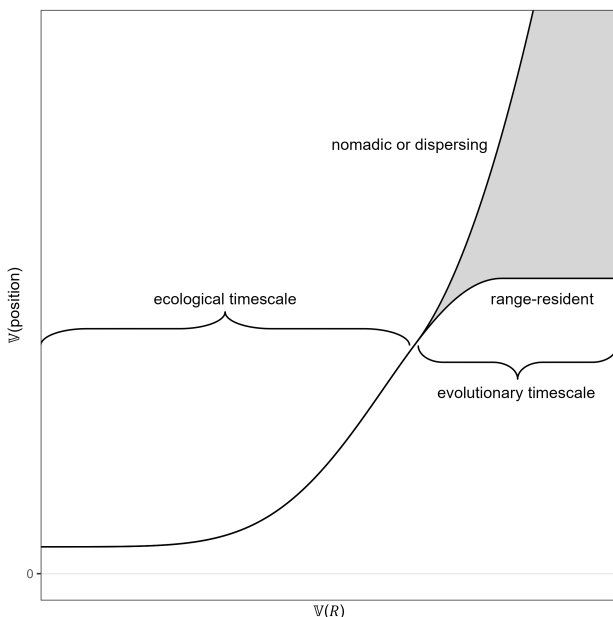


Figure 3: Hypothesized spatial needs (indicated as positional variance, $V(\text{position})$) of an animal as a function of resource unpredictability ($V(R)$). We expect low values of $V(R)$ to result in low $V(\text{position})$ as animals are able to depend on somewhat predictable resources. As $V(R)$ increases, spatial needs should increase nonlinearly, whether this results in an expansion of the home range (in the case of range-resident animals) or a switch to dispersal, nomadism, or migration. Note that the relationship between $V(R)$ and $V(\text{position})$ cannot be linear because it would require $V(\text{position})$ to be negative for low values of $V(R)$.

Similarly to the effect of $\mathbb{E}(R)$, we expect $\mathbb{V}(R)$ to have a nonlinear effect on animals' spatial needs. When $\mathbb{V}(R)$ is low enough that R is relatively predictable, we do not expect changes in $\mathbb{V}(R)$ to have a noticeable effect, but as resources become increasingly unpredictable, we expect spatial needs to increase progressively faster (figure 3). This is because as $\mathbb{V}(R)$ increases, the chances of finding low R increase superlinearly. Additionally, stochastic environments tend to be less productive (@ Chevin et al. 2010), and the added movement required to search for food increases animals' energetic requirements. If resources remain highly unpredictable over long periods of time (e.g., multiple lifespans), animals may evolve or develop new behaviors (such as nomadism, dispersal, and migration) or adaptations (such as increased fat storage, food caching, torpor, and hibernation).

When the unpredictability in R changes over time (figure 4a), changes in $\mathbb{V}(R)$ may have an appreciable effect on the location's favourableness. In this scenario, we can define $\mathbb{V}(R)$ as a function of time using the notation $\mathbb{V}(R) = \sigma^2(t)$ (figure 4b). When both $\mathbb{E}(R)$ and $\mathbb{V}(R)$ change over time, accurately and precisely predicting R becomes more complex (figure 4c-d).

Most habitats with appreciable seasonal changes in climate will require models to account for changes in both $\mathbb{E}(R)$ and $\mathbb{V}(R)$, as they often change within and between years, and periods of high productivity can often be more variable than times of lower productivity or dormancy. During times of resource unpredictability, animals will likely

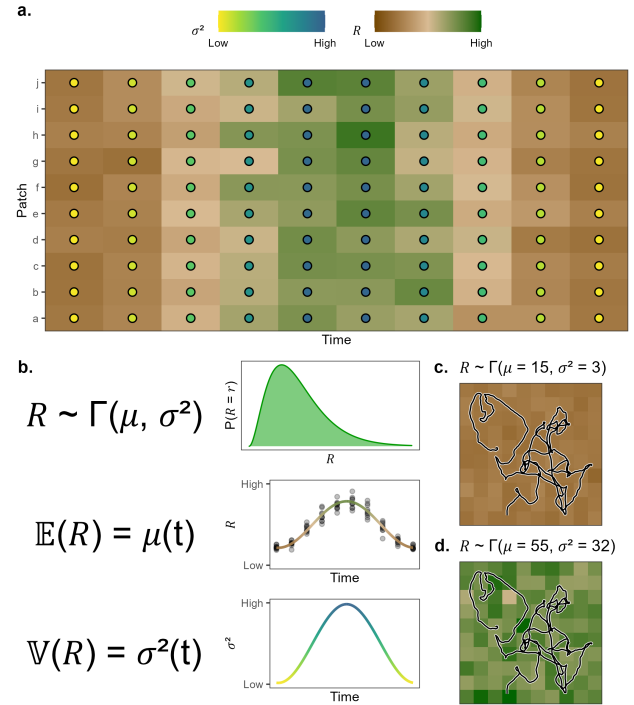


Figure 4: Fictitious example of variation in resource abundance in a heterogeneous environment with changing variance (even after accounting for changes in mean abundance). (a.) Although resource abundance (R , brown-green fill) varies over time and space, variance (dot color) is lowest at the beginning and end of the observational period and highest when R peaks. (b.) Arbitrary definition of R as following a Gamma distribution with mean μ and variance σ^2 . (c.) Simulated animal movement at a time of lowest $\mathbb{E}(R)$ and $\mathbb{V}(R)$. (d.) Simulated animal movement at a time of peak $\mathbb{E}(R)$ and $\mathbb{V}(R)$.

have higher spatial needs, particularly if they need to collect and store resources for periods scarcity or increased energetic needs. These include higher energetic needs during reproductive periods, whether this be due to pregnancy (Schmidt et al. 2020), to feed offspring (Saraux et al. 2011), or because the animal’s needs change over time (e.g., male deer growing antlers: French et al. 1956; Smolko et al. 2022). Failing to account for changes in $\mathbb{V}(R)$ can result in serious underestimations of animals’ spatial needs, which may lead to decreases in the fitness and size of a population while also increasing the risk of population collapse and human-wildlife conflict (Mukeka et al. 2019).

The effects of $\mathbb{V}(R)$ on animals’ spatial needs likely vary between species, since energetic and nutritional needs vary between species (Boratynski 2020; Noonan et al. 2020). Small-scale variations may be sufficient to causes changes in behavior for some small animals, while animals with larger spatial needs may not even notice a change. Rizzuto et al. (2021) found that the 50%, 75%, and 90% utilization distributions of snowshoe hares (*Lepus americanus*) increased with average C:N in lowbush blueberry as well as the coefficient of variation (i.e., standard deviation over mean) in C:N, which suggests that the hares expanded their home range in response to both nitrogen abundance and nitrogen variability. Similarly, Mueller et al. (2011) demonstrated that ungulates in more variable ecosystems move more and are more likely to be nomadic. In contrast, Lucherini and Lovari (1996) found that red foxes (*Vulpes vulpes*) living in areas with more more heterogeneous habitats required exponentially less space than foxes that lived in more homogeneous regions. Similarly, Herfindal et al. (2005) found that the home ranges Canadian lynx (*Lynx canadensis*) decreased with seasonality. A subsequent analysis by Nilsen et al. (2005) with the lynx data of Herfindal et al. (2005) along with data on wolverines (*Gulo gulo*), bobcats (*Lynx rufus*), and coyotes (*Canis latrans*), found that carnivores respond differently to resource variability and seasonality, although it is worth disentangling the effects of heterogeneity (i.e., changes in $\mathbb{E}(R)$) and and stochasticity ($\mathbb{V}(R)$).

Nilsen et al. (2005) also demonstrate that the effect of $\mathbb{V}(R)$ on the home range size of

wolves (*Canis lupus*) and fishers (*Martes pennanti*) depends on $\mathbb{E}(R)$. Therefore, it is not only important to account for both $e(R)$ and $\mathbb{V}(R)$ but also interaction effects between the two. It is also worth noting that carnivores may be more susceptible to $\mathbb{V}(R)$ since animal prey’s ability to move makes their abundance and location less predictable than those of plants. Since, the effects of $e(R)$ and $\mathbb{V}(R)$ may also affect prey abundance, it is important to account for both $e(R)$ and $\mathbb{V}(R)$ as well as any interactive effects between the two and how the effects may vary between animals with different diets or from different trophic levels, since animals from higher trophic levels will be affected by the cascading effects of $\mathbb{E}(R)$ and $\mathbb{V}(R)$ on each of the lower trophic levels (Harestad and Bunnell 1979; Noonan et al. 2020).

Interactive effects of $\mathbb{E}(R)$ and $\mathbb{V}(R)$

In habitats where both $\mathbb{E}(R)$ and $\mathbb{V}(R)$ change substantially over time, models should account for not only the effects of $\mathbb{E}(R)$ and $\mathbb{V}(R)$ separately, but also their interactive effects. A highly unpredictable habitat may be very inhospitable if resources are poor, but $\mathbb{V}(R)$ will have little effect if resources are always sufficiently abundant. Thus, we expect $\mathbb{V}(R)$ to have a stronger effect on spatial needs when $\mathbb{E}(R)$ is low, and less of an effect when $\mathbb{E}(R)$ is high.

Figure 5 illustrates simulated spatial requirements as a function of $\mathbb{E}(R)$ and $\mathbb{V}(R)$. The top row (constant $\mathbb{V}(R)$) shows how simulated spatial needs vary for different trends in $\mathbb{E}(R)$ while $\mathbb{V}(R)$ remains constant. As $\mathbb{E}(R)$ increases at a constant slope (linear $\mathbb{E}(R)$) the spatial needs decrease nonlinearly, with larger changes when $\mathbb{E}(R)$ is low, until home range size approaches the minimum size required by the animal. As described in the section on $\mathbb{E}(R)$, the nonlinear decrease is because changes in $\mathbb{E}(R)$ have a larger effect when $\mathbb{E}(R)$ is low. Additionally, the 95% home range is more sensitive to changes in $\mathbb{E}(R)$ than the core home range simply because larger quantiles (e.g., 95% > 50%) are more sensitive to changes in the distribution. Additionally, when $\mathbb{E}(R)$ is lower, $\mathbb{V}(H)$ is higher (particularly for the 95% quantile), since resource-poor regions force animals to move more, which results in a

greater uncertainty in a longer and thus also more unpredictable search.

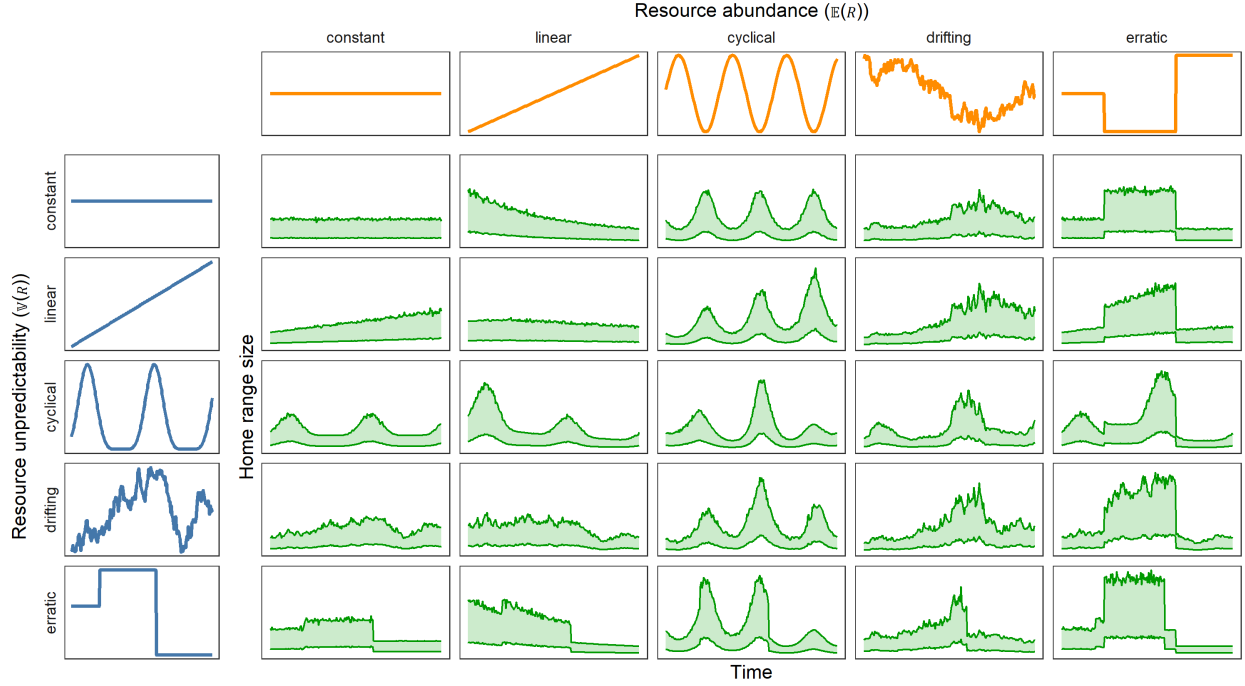


Figure 5: Simulated spatial requirements for animals living in habitats where the mean and variance in resource abundance (R) are constant, linearly increasing, cyclical, drifting, or erratic over time. The lower green line indicates the animal’s core home range (50% quantile), while the top line indicates the 0.95 utilization quantile. Note how both quantiles decrease nonlinearly as $\mathbb{E}(R)$ increases, and they increase nonlinearly as $\mathbb{V}(R)$ increases. Additionally, the variance in both quantiles is higher when $\mathbb{V}(R)$ is higher, and changes in $\mathbb{V}(R)$ have greater impacts when $\mathbb{E}(R)$ is low. Simulations were run such that animals followed the same 1000 tracks at each time point starting from the location $\langle 0, 0 \rangle$ until they reach satiety, after which they returned to $\langle 0, 0 \rangle$ over the same amount of time required to reach satiety. The animal’s home range was then estimated using an Ornstein-Uhlenbeck Foraging (OUF) model via the `ctmm` package (Fleming and Calabrese 2021).

In regions where the average resource abundance changes over time (e.g., seasonal changes – see cyclical $\mathbb{E}(R)$ and Lai et al. 2017), animals should have access to sufficient space to fulfill their needs during periods of scarcity, whether the space available is sufficiently large year-round or it changes seasonally with the expected changes in $\mathbb{E}(R)$ (e.g., winter park closures). However, estimates of spatial requirements based on estimated changes in $\mathbb{E}(R)$ should be interpreted carefully, since model error and unforeseeable decreases in $\mathbb{E}(R)$ (such as following fires or floods) may increase animals’ spatial needs suddenly and unpredictably. Thus, it is best to include a “buffer” area so the available space is larger than the estimated spatial needs. This is particularly the case in environments where resource abundance changes unpredictably (drifting $\mathbb{E}(R)$), since accurate long-term estimates of $\mathbb{E}(R)$ may be hard to produce, if not impossible. In cases where $\mathbb{E}(R)$ is highly unpredictable, animals should have enough space to collect resources during times of greatest predicted scarcity, particularly if

the changes in resource abundance occur rapidly, often, or for long periods of time (erratic $\mathbb{E}(R)$).

The leftmost column of figure 5 (constant $\mathbb{E}(R)$) illustrates the effects of $\mathbb{V}(R)$ on the simulated spatial needs while $\mathbb{E}(R)$ remains constant. Overall, both quantiles increase with $\mathbb{V}(R)$, although $H_{95\%}$ is more sensitive to changes in $\mathbb{V}(R)$ than $H_{50\%}$, as with changes in $\mathbb{E}(R)$. Additionally, note how both H and $\mathbb{V}(H)$ increase with $\mathbb{V}(R)$ (e.g., constant $\mathbb{E}(R)$, linear $\mathbb{V}(R)$). This is because, similarly to resource-poor areas, more stochastic times require the animal to move for longer periods of time, which results in a greater uncertainty in how much time and space it will require to reach satiety.

The remaining panels in figure 5 illustrate how the effect of $\mathbb{V}(R)$ depends on $\mathbb{E}(R)$ (and vice-versa) as well as how complex the relationships can be. Since $\mathbb{E}(R)$ and $\mathbb{V}(R)$ have opposite effects on H , disentangling the effects can be particularly difficult when both parameters change monotonically, especially when the trends are linear (i.e., linear $\mathbb{E}(R)$ and $\mathbb{V}(R)$). When both $\mathbb{E}(R)$ and $\mathbb{V}(R)$ increase linearly, the change in $H_{95\%}$ is small and not monotonic, while there is no clearly visible change in $H_{50\%}$. However, when $\mathbb{E}(R)$ changes nonlinearly (e.g., cyclical $\mathbb{E}(R)$ with linear $\mathbb{V}(R)$), it is easy to see how the increase in $\mathbb{V}(R)$ amplifies the effects of $\mathbb{E}(R)$ (and vice-versa). Similarly, the effect of $\mathbb{V}(R)$ is stronger when $\mathbb{E}(R)$ is low (e.g., linear $\mathbb{E}(R)$ with cyclical $\mathbb{V}(R)$). Thus, the estimated spatial needs are largest when $\mathbb{E}(R)$ is low and $\mathbb{V}(R)$ is high, and they are smallest when $\mathbb{E}(R)$ is high and $\mathbb{V}(R)$ is low (see the panel with cyclical $\mathbb{E}(R)$ and $\mathbb{V}(R)$ as well as Lai et al. 2017).

Not all 25 scenarios depicted in figure 5 may be realistic, but the trends in $\mathbb{E}(R)$ and $\mathbb{V}(R)$, and their impacts on animal space use are useful examples that can be thought of as simplified scenarios. $\mathbb{E}(R)$ and $\mathbb{V}(R)$ can be assumed to be (approximately) constant in highly homogeneous environments, or environments where resources are sufficiently abundant that changes in $\mathbb{E}(R)$ and $\mathbb{V}(R)$ are relatively small and remain undetected. Although it is impossible for $\mathbb{E}(R)$ and $\mathbb{V}(R)$ to increase linearly forever, such increases may be possible for short periods of time (followed by periods of no change or decrease). Cyclical oscillations

in $\mathbb{E}(R)$ and $\mathbb{V}(R)$ may occur in urban environments as human activity changes within and between days (Péron et al. 2017; Ikeda et al. 2022) and as temperatures fluctuate daily and seasonally (Geremia et al. 2019; Alston et al. 2020), while $\mathbb{E}(R)$ and $\mathbb{V}(R)$ may drift randomly in highly complex environments which are too hard to predict. Finally, erratic changes in $\mathbb{E}(R)$ and $\mathbb{V}(R)$ may occur in environments where changes are very sudden, such as areas prone to fires or floods, as well as habitats with drastic human alteration (e.g., a forest which is clear-cut with a subsequent artificial re-forestation). However, if stochastic changes are sufficiently small and frequent, animals may perceive them as continuous and smooth changes rather than a series of small and sudden changes. Estimating trends in $\mathbb{E}(R)$ and $\mathbb{V}(R)$ requires animals have high cognitive capacity, since distinguishing between changes in $\mathbb{E}(R)$ and $\mathbb{V}(R)$ is not easy (Steixner-Kumar and Gläser 2020), especially if $\mathbb{E}(R)$ and $\mathbb{V}(R)$ are not independent, as in the case of $R \sim \Gamma(\mu(t), \sigma^2(t))$.

Although the trends in figure 5 are complex and the effects of $\mathbb{E}(R)$ and $\mathbb{V}(R)$ do not seem easy to disentangle, both $\mathbb{E}(R)$ and $\mathbb{V}(R)$ affect spatial needs as we hypothesized (figure 6). In the following discussion section, we detail how this framework can be applied to empirical data and used for conservation decision-making.

Discussion

This paper presents a new unifying framework for estimating the effects of resource abundance and stochasticity on animals’ spatial needs. The hypotheses and methods we present allow researchers to generalize the effects $\mathbb{E}(R)$ and $\mathbb{V}(R)$ have on animals’ spatial needs by building upon previous work rather than stating their results as *de novo* findings. Instead, one can test whether members of the same population or species behave similarly, and whether all members of the group have a common functional response using hierarchical models (Pedersen et al. 2019). Individuals and populations that were thought to have different behaviors and spatial needs may instead have a single common behavior as they

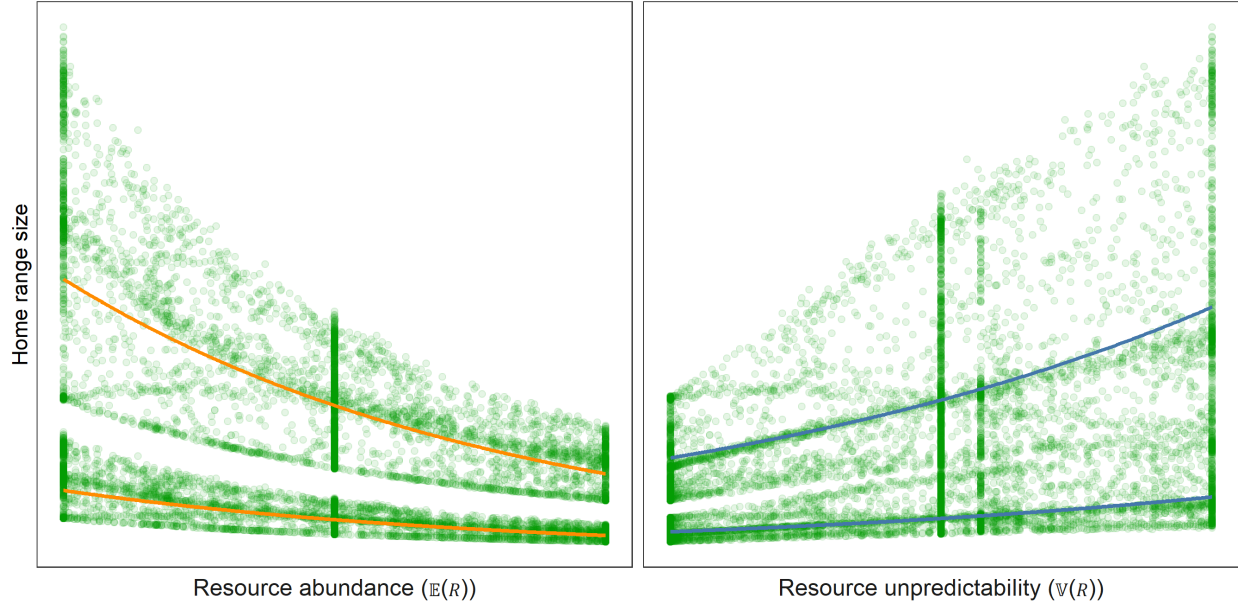


Figure 6: Effects of $\mathbb{E}(R)$ and $\mathbb{V}(R)$ on simulated spatial requirements. The relationships were estimated using a Generalized Linear Model with a Gamma family of distributions that accounted for the effects of both $\mathbb{E}(R)$ and $\mathbb{V}(R)$ as well as differences between the two quantiles. The bottom line indicates the relationships with the animal’s core home range (0.5 quantile), while the top line indicates the relationship with the 0.95 utilization quantile. Note the nonlinear decrease in both utilization quantiles as $\mathbb{E}(R)$ increases and the nonlinear increase in both utilization quantiles as $\mathbb{V}(R)$ increases.

respond to $\mathbb{E}(R)$ and $\mathbb{V}(R)$ following the same functional response (**examples?**).

In this discussion section, we make considerations about the effects of $\mathbb{E}(R)$ and $\mathbb{V}(R)$ on various animal adaptations, including movement behaviors, energy storage, and spatiotemporal memory. We then illustrate how one may apply this framework to their own data by providing an empirical example using tracking data on a lowland tapir (*Tapirus terrestris*) from the Brazilian Cerrado. Finally, we demonstrate how to use this framework to create products that can inform conservation-based decisions, including predicting animals’ spatial needs and assessing the quality of potential (and current) conservation areas.

Animal adaptations to changes in $\mathbb{E}(R)$ and $\mathbb{V}(R)$

The spatiotemporal scales over which an event occurs are a main determinant of whether an animal will be able to predict the event and how it will respond to it (or fail to do so). Events which occur at the scale of the organism (i.e. approximately one or more times per lifetime and within the animal’s spatial range, see Frankham and Brook 2004) are more likely to be perceived as a threat or boon worth preparing for (e.g., elephants: Foley et al. 2008; bison

and mule deer: Geremia et al. 2019). Smaller and short-lived organisms (e.g., mice) are more likely to be severely impacted by stochastic events than larger ones (e.g. elephants), since larger organisms can have bigger energy reserves (Lindstedt and Boyce 1985), can move longer distances over short periods of time (Hirt et al. 2017), and tend to have longer lifespans, generation times, and developmental periods (Brown et al. 2004) that allow them to adapt their behavior to such events, including the development of memory (framework: Riotte-Lambert and Matthiopoulos 2020; elephants: Foley et al. 2008; Polansky et al. 2015; bison and mule deer: Geremia et al. 2019; Rickbeil et al. 2019; elk: Falcón-Cortés et al. 2021; blue whales: Abrahms et al. 2019).

The short generation time and high reproductive rate of smaller, *r-selected* species (Pianka 1970; Brown et al. 2004) may also promote traits that increase survival following frequent extreme events by increasing population survival rates through higher population size, dispersal, and genetic diversity (**examples?**). Events that occur over large spatiotemporal scales can promote slow changes through adaptation, natural selection, and evolution (Gienapp et al. 2008; Logares and Nuñez 2012; Anderson et al. 2017; Grant et al. 2017), which are numerically more likely if the starting population is large with abundant offspring (**examples?**; but see Leung 2022).

Events which occur multiple times at relatively predictable intervals during an animal’s lifespan and over multiple generations (such as the alternating of seasons) allow the animal to anticipate times of scarcity and prepare for them by, for instance, increasing its fat storage (marmots: Armitage et al. 2003; bears: Nespolo et al. 2022), caching resources (Post et al. 2006), or migrating (Mueller et al. 2013; Geremia et al. 2019). Of course, an animal with a lifespan shorter than a year will be unable to perceive the cyclical alternating of the seasons, and an animal with a lifespan of a few weeks or days may not even experience substantial changes in weather and temperature other than lower temperatures at night than during the day.

When an animal’s expected lifespan is longer than a year, preparing for predictable times

of abundance and scarcity becomes an advantage (and often a necessity). In such cases, animals can increase their chances of survival via physiological and behavioral adaptations, including adapting the timing of reproduction (ref?) and torpor (marmots: Inouye et al. 2000; ground squirrels: Goldberg and Conway 2021), as well as memory (Fagan et al. 2013; framework: Riotte-Lambert and Matthiopoulos 2020; roe deer: Ranc et al. 2022; caribou: Cavedon et al. 2022; elk: Falcón-Cortés et al. 2021; elephants: Polansky et al. 2015), which is required for migration (butterflies: Stefanescu et al. 2021; whooping cranes: Mueller et al. 2013; bison and mule deer: Geremia et al. 2019; mule deer: Merkle et al. 2019; blue whales: Abrahms et al. 2019; Middleton et al. 2018; elk: Rickbeil et al. 2019). However, relying on environmental cues rather than on memory alone (Büntgen et al. 2017; Rickbeil et al. 2019; ungulates: Severson et al. 2021; birds: Jonzén et al. 2006), can prevent animals from becoming trapped in sub-optimal conditions (Abrahms et al. 2019).

An animal’s fitness and chances of survival in a changing environment depend strongly on its adaptability and responsiveness to change (Riotte-Lambert and Matthiopoulos 2020). An animal’s ability to recognize cues that precede extreme events or periods of scarcity or abundance can have appreciable effects on the animal’s chance of survival and reproduction. For example, ungulates’ ability to time their yearly migrations on available forage biomass, snow fall, snow melt, and hunting pressure allow them to adapt to changes in both $\mathbb{E}(R)$ and $\mathbb{V}(R)$, while their spatial memory (Falcón-Cortés et al. 2021; Ranc et al. 2022) allows them to optimize their large-scale movement by reducing the amount of time and energy spent exploring. Similarly, the ability of trans-Saharan migrant birds to adapt their migration timing based on environmental cues allows them to account for differences $\mathbb{E}(R)$ between years (Jonzén et al. 2006). However, relying strongly on short-term changes rather than depending on memory can also cause animals to fail to find crucial resources (Foley et al. 2008; Polansky et al. 2015).

Recent changes in climate during the last few decades have caused some species to shift their ranges (terrestrial animals: Chen et al. 2011; Büntgen et al. 2017; ungulates: Severson

et al. 2021), including migratory animals (**examples?**). While range shifts can help species overcome changing conditions, they can still result in phenological mismatches (Lameris et al. 2018), and they also add pressure to the species that already live in the habitat. Additionally, specialists and obligate symbionts are less likely to shift their range since it is determined by their food sources’ and associates’ ability to move and adapt, too. Consequently, the arrival of new species may exacerbate the stressors such animals are already facing.

Applying this framework

The hypotheses we present here allow researchers to combine findings and generalize results to a single, common set of functional responses. We expect the two hypotheses we present here (figures 1 and 3) to be applicable to all animals, once differences in metabolic needs and diet are accounted for. In this subsection, we illustrate how researchers can test these hypotheses using their own data to build on previous work rather than listing the results as *de novo* findings. Additionally, the analyses can be expanded to test whether members of the same population or species behave according to common functional responses to $\mathbb{E}(R)$ and $\mathbb{V}(R)$ while also quantifying any deviation from the hypothesized behavior. In the following sections, we illustrate how one can apply this framework to empirical data.

We start by providing examples and considerations on how one may model R , animals’ spatial needs, and the effects of $\mathbb{E}(R)$ and $\mathbb{V}(R)$ on animals’ spatial needs. Next we provide an empirical example using tracking data on a lowland tapir (*Tapirus terrestris*) from the Brazilian Cerrado and NDVI as a proxy for R . Finally, we offer suggestions on how this approach can be used to inform conservation-related decisions, including assessing habitat quality and estimating animals spatial needs under different scenarios.

Modeling R

Location-scale models (Rigby and Stasinopoulos 2005; Stasinopoulos and Rigby 2007) are a class of statistical models that allow us to estimate changes in a random variable’s mean

(i.e. its location) and variance (which depends on its scale) while allowing the mean-variance relationship to vary. **mgcv** (Wood 2017) is a commonly-used R package that allows one to fit Generalized Linear Models (GLMs, see Zuur 2009) and generalized additive models (GAMs, see Wood 2017), including location-scale GLMs and GAMs. Currently, the **mgcv** package allows one to fit location-scale models with a variety families of distributions, including Gaussian (i.e., normal), scaled t, gamma, Tweedie, and Gumbel.

The Gaussian family of distributions is the most flexible, since the mean and standard deviation parameters are assumed to be independent, and the response can be either positive or negative. The scaled t family is similar to the Gaussian family, but it is best for high-variance data with heavy tails. However, the two distributions' flexibility can also result in unreliable estimates for non-Gaussian responses, such as strictly positive data (e.g. area), count data, proportions (e.g., percentage of forested habitat), NDVI (Pettorelli et al. 2011), and extremes (such as daily maximum or minimum temperatures).

The Gamma location-scale family is best for strictly positive responses, such as areas (including home ranges), elemental compositions (e.g., carbon to nitrogen ratio, see Rizzuto et al. 2021), total biomass (e.g., kg of carbon per m²), or energetic intake (e.g., kcal/day). The Tweedie family is similar to the Gamma family, but it allows for zero data, so it is appropriate for data with a non-trivial amount of zeros, such as daily precipitation or prey abundance. Lastly, the Gumbel distribution is suitable for modeling the extremes of a distribution, such as maximum or minimum daily temperatures.

If one is interested in using other families of distributions, including zero-inflated and hurdle models, we suggest using the **brms** package (Bürkner 2017), which allows full control over all of the family's parameters using a fully Bayesian approach (Bürkner 2018). In this paper, we use the **mgcv** package because although **brms** provides more flexibility and a greater choice of families, its computational costs can be prohibitive for large datasets, particularly for location-scale models.

Irrespective of whether one uses a frequentist or Bayesian approach, it is important to

model the mean and variance terms carefully. Since trends in both $\mathbb{E}(R)$ and $\mathbb{V}(R)$ can be nonlinear and nonmonotonic, we suggest using a GAM rather than a GLM. However, the complexity of the spatio-temporal terms should be chosen carefully, particularly for mean term. An excessively wiggly $\hat{\mu}(t)$ will cause $\widehat{\sigma^2}(t)$ to be under-estimated and under-fit, and an excessively smooth $\hat{\mu}(t)$ will inflate $\widehat{\sigma^2}(t)$. Thus, models should be fit with care to avoid inaccurate estimates. Although there is no error-proof system, choosing the complexity of the terms based on the animal’s ability to detect change and adapt should be sufficient. Additionally, using REstricted Marginal Likelihood (REML, a form of penalized maximum likelihood optimization, see Wood 2011) and setting the basis dimension (\mathbf{k}) of the scale terms to be half or less than that of the mean terms should provide reasonably accurate results. We suggest starting with low values of \mathbf{k} and adjusting \mathbf{k} based on the trends in the residuals. Note that since R is likely spatiotemporally autocorrelated, it may be easy to overfit the model if R is measured at high frequencies and with a large sample size (but low effective sample size).

Modeling spatial needs

Recent improvements in animal tracking technologies (e.g., increasing sampling duration and frequency of GPS units) have allowed scientists to demonstrate that changes in animals movement and behavior may be more common than previously thought (leatherback turtles: Hays et al. 2006; arctic foxes: Lai et al. 2017; elephants: Foley et al. 2008; bison and mule deer: Geremia et al. 2019; bald eagles: Wheat et al. 2017, 2017). However, most commonly-used movement models assume animals’ behaviors to remain consistent during the entirety of the tracking period (but see state-space models, e.g., Polansky et al. 2015).

To quantify an animal’s changes in behavior in response to $\mathbb{E}(R)$ and $\mathbb{V}(R)$, we suggest using a **sliding window** approach. The width of the window, w , should be a fixed value greater than two or three times the animal’s expected range crossing time (**ref?**). If the animal’s spatial use is relatively consistent over time, one may fit a movement model to the

whole dataset, and then choose w based on the model’s τ_p . Alternatively, if the animal’s behavior changes repeatedly (e.g., uses a small area for a short period of time before moving to a new one), then one may want to test multiple values of w to find a value sufficiently large for an effective sample size of 2 or 3 range crossings (i.e., $w \approx 2.5 \tau_p$). Modeling animal movement as a continuous-time stochastic process is particularly useful in this approach, since it accounts for the uncertainty and limited amount of information contained in short periods of (autocorrelated) tracking data by differentiating between the sample size (i.e., the number of locations) and effective sample size (i.e., the number of range crossings, see Noonan et al. 2019a, 2019b). In this paper, we model tracking data using continuous-time movement models via the `ctmm` package (Fleming and Calabrese 2021) for R (R Core Team 2022).

Modeling effects of $\mathbb{E}(R)$ and $\mathbb{V}(R)$

As discussed in the section on modeling R , the first step to modeling H is to choose an appropriate distribution. Since H is strictly positive and continuous, a Gamma distribution seems the most appropriate among the distributions currently offered by the `mgcv` package (Wood 2017). The Tweedie distribution would also be appropriate if the mean-variance relationship of the Gamma distribution does not fit the data well.

The decrease in $\mathbb{V}(H)$ as $\mathbb{E}(R)$ increases and as $\mathbb{V}(R)$ decreases in figure 6 suggests that a location-scale model is likely required. If there is not sufficient data to fit a location scale model (which is not the case here), a simple Gamma model may be sufficient, but we suggest selecting the best distribution using an information criterion such as the Akaike Information Criterion (AIC, see Akaike 1974). While a GAM would allow the effects of $\mathbb{E}(R)$ and $\mathbb{V}(R)$ on H to be quite flexible, we suggest using a GLM rather than a GAM (unlike when modeling R) because we expect the relationship to be fairly simple and monotonic. Additionally, restricting the model to a GLM reduces the risk of issues that may arise due to limited sample size and temporal autocorrelation in $\mathbb{E}(R)$ and $\mathbb{V}(R)$. If one interested in

fitting a GAM but imposing shape restrictions, such as monotonicity, we suggest using the `scam` package (Pya 2022).

An empirical example: Lowland tapir in the Brazilian Cerrado

In this section, we use empirical tracking data on a lowland tapir (*Tapirus terrestris*) from the Brazilian Cerrado to show how this framework can be applied to better understand the movement ecology of free-ranging animals. We estimate $\mathbb{E}(R)$ and $\mathbb{V}(R)$ by modeling NDVI (Pettorelli et al. 2011) using a location-scale Gaussian GAM. Although a beta model would be more appropriate, the `mgcv` package does not currently support location-scale beta models. While the `brms` model supports beta location-scale models, the dataset is sufficiently large and with data sufficiently away from the boundaries (i.e., -1 and 1) that we expect the estimates to be reasonably accurate for an illustrative example. Additional information regarding the modeling can be found in Appendix 2.

Figure 7 illustrates the tapir’s response to changes in $\mathbb{E}(R)$ and $\mathbb{V}(R)$. Panel **a** provides an overview of the tracking data, while panels **b** and **c** show the changes in mean and variance in NDVI, respectively. Panel **d** shows the changes in the tapir’s spatial use over time. Note how the home range size is larger during periods of lower average NDVI (e.g., August 2017) and smallest during periods with high NDVI (January 2018), despite an increase in the variance in NDVI. In contrast, when resources are scarce and highly unpredictable (August 2018), the tapir uses up to 5 times more space than when resources are abundant and predictable. Finally, panels **e** and **f** show that the tapir’s spatial needs change based on the simple relationships we hypothesized (figures 1 and 3) and supported with the simulated responses (figure 6).

Applications for conservation

The designation of high-quality habitats is a central concern of many conservation initiatives. This framework allows consultants and conservation managers to quantify the quality of a

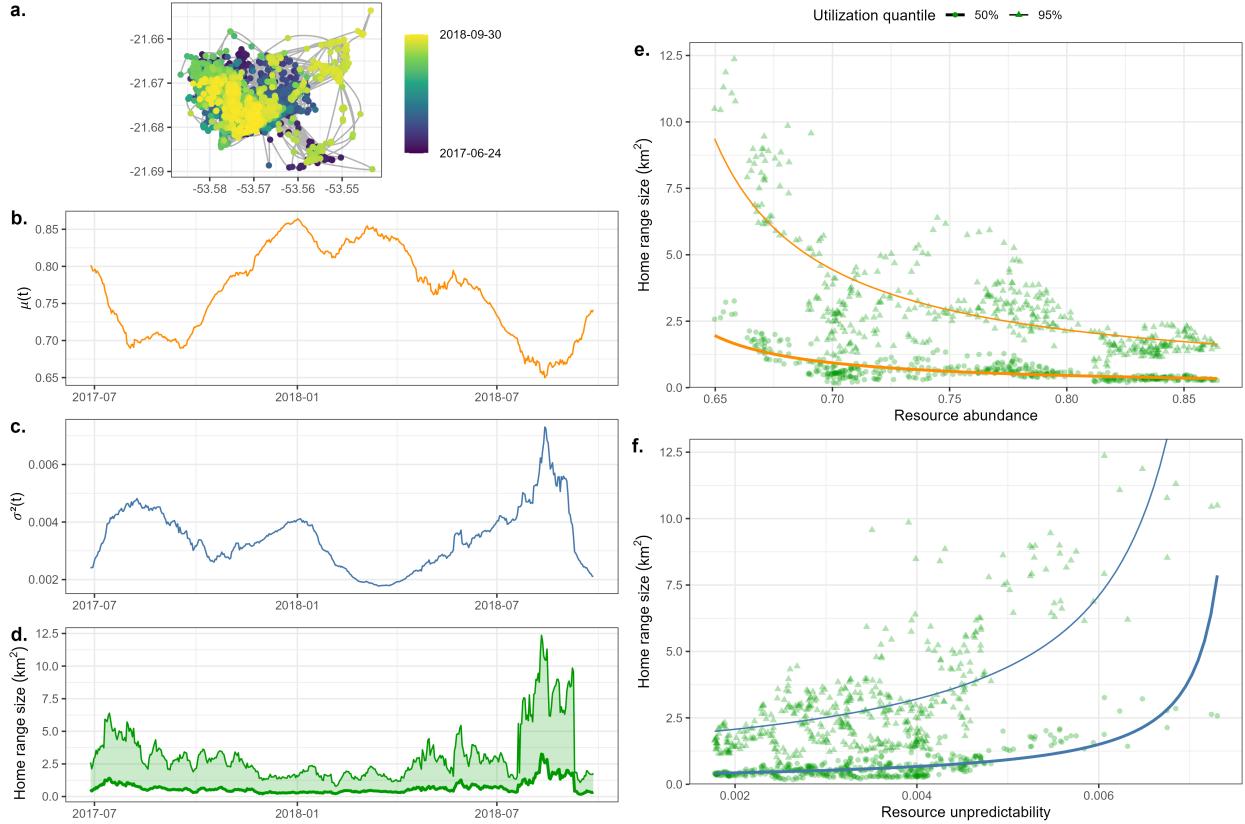


Figure 7: Seven-day home range size of a tapir (*Tapirus terrestris*) in response to changes in mean and variance in resource abundance. (a.) GPS tracking data of the tapir. (b.) Mean resource abundance estimated as the mean NDVI at the locations visited by the tapir. (c.) Variance in resource abundance estimated as the average variance in NDVI at the locations visited by the tapir. (d.) Estimated home range size during each seven-day period, based on 50% and 95% utilization quantiles. (e.) Effect of resource abundance on home range size. (f.) Effect of resource unpredictability on home range size. The effects in panels e and f were estimated using two generalized linear models with Gamma families of distributions. Although a single model would be ideal, the small sample size and collinearity between $\mathbb{E}(R)$ and $\mathbb{V}(R)$ prevent us from estimating accurate effects of $\mathbb{E}(R)$ and $\mathbb{V}(R)$ within the same model (see Appendix 2). The tapir movement data corresponds to the individual named "Anna" from the Cerrado sample of Medici *et al.* (2022).

habitat based on its resource abundance and stochasticity while also estimating the amount of space animals would need in the habitat. With the methods presented in this paper, one can assess the quality of current protected areas and predict whether or not the areas will be sufficiently large or appropriate in future decades while also evaluating new potential conservation areas. In light of Canada’s pledge to conserve 30% of its landmass and waters by 2030 (ref?), the framework and methods presented here provide useful metrics for maximizing the quality and stability of protected areas while estimating their quality in the decades to come under various climate change scenarios (ref?).

Accounting for changes in resource abundance and resource stochasticity (e.g, between seasons or “good” and “bad” years) allows researchers and conservation managers can ensure the quality of protected areas is sufficiently high to sustain biodiversity long term. Protecting areas with high resource abundance and low resource unpredictability will minimize animal’s spatial needs while also increasing the stability in resiliency in spatial needs, since changes in spatial needs are more drastic when $\mathbb{E}(R)$ is low or $\mathbb{V}(R)$ is high (figure 6, panels e and f).

need to add a few more ideas?

Conclusion

The work presented here provides a unifying framework for viewing animal movement as a function of resource abundance. We provide realistic and flexible hypotheses of the effects of $\mathbb{E}(R)$ and $\mathbb{V}(R)$ on animals' spatial needs and movement behavior. We demonstrate that animals' spatial needs respond nonlinearly to both resource abundance and stochasticity, and we demonstrate the importance of accounting for $\mathbb{V}(R)$ besides $\mathbb{E}(R)$. We also provide a way of modeling animal movement continuously rather than imposing arbitrary thresholds between different types of behaviors, including temporal changes in spatial needs and shifts between range-residency and nomadism). The methods presented here can be applied to assess the current and future quality of protected areas while also estimating the amount of space animals currently need and will need in the future under different climate change scenarios.

MISC

Extreme events (Logares and Nuñez 2012; Anderson et al. 2017) such as heat domes (Emerton et al. 2022), hurricanes (Widmer et al. 2004); severe storms (Berger et al. 2018), fires (Ruthrof et al. 2016), new diseases (Murray et al. 2006; Hollings et al. 2014; Hoyt et al. 2021), and anthropogenic die-offs (Matkin et al. 2008) are important events which are hard to predict (i.e., highly stochastic) and can cause great population instability by drastically reducing the size and genetic diversity of a population (Reed et al. 2003; Ameca y Juárez et al. 2012). Managing the intensity of and frequency of extreme events (e.g., Aponte et al. 2016) can increase the stability of a habitat while promoting habitat diversity and adaptations to the event (Staver et al. 2011; Tingley et al. 2016; Nimmo et al. 2019).

Mueller et al. (2013): Whooping Cranes migrate better when there are elders

Other empirical refs to possibly add: Wolkovich et al. (2012), Nathan et al. (2022)

Simulation refs: Cain (1985), Blackwell (2007), Quaglietta et al. (2019), Tucker et al. (2021)

Patch connectivity and ease of movement may widen HRs by decreasing the energetic cost of movement and favoring exploration (Dickie et al. 2022), or they may shrink HRs by decreasing the energetic cost of movement while increasing encounter rates with resources (Visser and Kiørboe 2006; Bartumeus et al. 2008; Martinez-Garcia et al. 2020).

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. (2022) found that the movement of tapirs (*Tapirus terrestris*) was unaffected by anthropogenic activity or habitat type.

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