

# How resource abundance and stochasticity affect animals' spatial needs

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# Contents

<b>Abstract</b>	<b>3</b>
<b>Introduction</b>	<b>4</b>
<b>Concepts and definitions</b>	<b>7</b>
Resources as a random variable . . . . .	7
Probability distributions . . . . .	7
Expected resource abundance, $\mathbb{E}(R)$ . . . . .	8
Variance in resource abundance, $\mathbb{V}(R)$ . . . . .	9
Simulating resource abundance . . . . .	9
Estimating resource abundance using NDVI . . . . .	9
Animal movement as a stochastic process . . . . .	10
Drivers of animal movement . . . . .	10
Visualizing movement as a stochastic process . . . . .	11
Quantifying spatial needs . . . . .	12
Advantages of modeling animal movement as a stochastic process . . . . .	13
Unassigned . . . . .	13
<b>Effects of <math>\mathbb{E}(R)</math></b>	<b>15</b>
<b>Effects of <math>\mathbb{V}(R)</math></b>	<b>18</b>
<b>Interactive effects of <math>\mathbb{E}(R)</math> and <math>\mathbb{V}(R)</math></b>	<b>22</b>
<b>Discussion</b>	<b>25</b>
Animal adaptations to changes in $\mathbb{E}(R)$ and $\mathbb{V}(R)$ . . . . .	27
Applying this framework . . . . .	29
Modeling $R$ . . . . .	30
Modeling spatial needs . . . . .	31
Modeling the relationships . . . . .	32
An empirical example: Lowland tapir in the Brazilian Cerrado . . . . .	33
Using this framework in conservation-related decisions . . . . .	34
<b>Conclusion</b>	<b>35</b>
<b>MISC</b>	<b>36</b>
<b>References</b>	<b>37</b>

## Abstract

Since animals need to maintain a positive energetic balance to grow and reproduce, their 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 in 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 resource abundance 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 probability to survive and reproduce. 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), or even death (Foley et al. 2008; Berger et al. 2018). Thus, many organisms will change 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), 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 (**refs?**), 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 hypothesis for the relationship between an animal's home range size is inversely proportional

to resource abundance. 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 and diet, as demonstrated over three decades ago by various scientists (Harvey and Clutton-Brock 1981, 1981; Gittleman and Harvey 1982; Lindstedt et al. 1986; Reiss 1988). 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 animal’s response to changes in resource abundance, there is little to no information on how many species respond to unpredictable changes in the resources they depend on.

A habitat’s long-term average 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 resource abundance, the differences in resource predictability 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 chapters. 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 of how animals respond to changes in resource abundance. Afterwards, we present a hypothesis for how animals respond to resource unpredictability. 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 (i.e., known observations or instances) of random variables, 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, 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 as  $\mu$ ) 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,  $t$ :  $\mathbb{E}(R) = \mu(t)$ .

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  $\mu(t)$ . 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  $(k, \theta)$  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  $\mu$  and  $\sigma^2$  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

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

where  $\nu$  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's 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  $\alpha$  and  $\beta$  such that the mean is  $\mu = \frac{\alpha}{\alpha+\beta}$  while the variance is  $\sigma^2 = \frac{\alpha\beta}{(\alpha+\beta)^2(\alpha+\beta+1)}$ ). 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  $\vec{u}_t$  to location  $\vec{u}_{t+1}$  using the model

$$\vec{u}_{t+1} = F(\Omega, \Phi, \vec{r}_t, \vec{w}_t, \vec{u}_t), \quad (2)$$

such that an animal's position as time  $t+1$  depends on its motion capacity ( $\Omega$ ), navigation capacity ( $\Phi$ ), internal state ( $\vec{w}_t$ ) and current location ( $\vec{u}_t$ ), as well as how each of the parameters may change with the current environmental factors ( $\vec{r}_t$ ). 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  $\Omega$ ,  $\Phi$ ,  $\vec{r}_t$ , and  $\vec{w}_t$  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. However, we can focus on animals' behavior and spatial

needs as a response to resource abundance and unpredictability alone (rather than measuring changes in each of an animal’s resources, needs, and behavioral states directly).

## Visualizing movement as a stochastic process

To understand how movement can be viewed as a stochastic process, imagine an animal that starts at its den and moves to collect food and other resources, and it returns to its den 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 exploring before returning “home” (or the time required for the position to “decay” back to the average position), which is often referred to as the **range crossing time** or the positional autocorrelation parameter,  $\tau_p$ . Similarly, we can define  $\tau_v$  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.  $\tau_v$  is referred to the animal’s **directional persistence** or the velocity autocorrelation parameter. Thus, 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 a variety properties of tracking data which are problematic for models that assume errors to be independent while also leveraging such properties to estimate important movement parameters. Accounting for autocorrelation in movement data (which is present in most modern datasets) avoids systematic biases in the estimation of home ranges (Noonan et al. 2019b) as well as path length and average (or instantaneous) speed (Noonan et al. 2019a).

If sampling frequency is too low to provide precise measures of autocorrelation, it will be inappropriate to estimate an animal’s average speed, directional persistence, and range crossing time, but the data can still provide reasonable estimates of the animal’s spatial needs

and usage, and model selection procedures with criteria such as AIC can help the analyst choose the most appropriate model for the available data (Silva et al. 2022). Estimates of average or instantaneous speed require the highest sampling frequency ( $\Delta t \lesssim \tau_v$ , 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, 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  $\tau_p$ , one can still obtain good estimates of the animal’s spatial needs and home range size, provided that the sampling duration is sufficiently long.

## 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 of animals that are not range-resident. ***but we can use a sliding window approach if animals are temporarily range resident or to estimate continuous changes in short-term spatial needs***

Although range-resident animals will generally have smaller  $\mathbb{V}(\text{position})$  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  $\tau_p$ ,  $\tau_v$ , and  $\bar{v}$  can help discriminate between different kinds of movement. Animals with a  $\tau_p$  shorter than a year are likely range-

resident, while animals with a  $\tau_p$  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  $\tau_p$  is on the order of its expected lifespan, it is most often nomadic, since it is unlikely to return to locations it visited in the past.

### **Advantages of modeling animal movement as a stochastic process**

Predicting animal movement using stochastic models may seem less straightforward and more complex than using deterministic models, but ignoring the causes and decisions that determine the movement allows us to focus more on the animal's movement and behavior and less on recognizing each cause of movement. 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).

Depending on sampling frequency, statistical methods that rely on straight-line displacement are prone to under-estimating the distance traveled by an animal and its speed at coarse sampling frequencies, while they over-estimate them at fine frequencies (Noonan et al. 2019a). In addition, most commonly-used methods for home range estimation assume tracking data to be independent of one another and sampled at consistent and discrete intervals, which is most often not the case. Consequently, animals' spatial needs are often under-estimated (Noonan et al. 2019b).

### **Unassigned**

Pretorius et al. (2020): flamingos – migrating or nomadic?

Boratyński (2020): animals' hr is limited by BMI and maximum metabolic rate, which

can be accounted for by accounting for body mass (Noonan et al. 2020)

Arechavala-Lopez et al. (2019): octopuses (*Octopus vulgaris*) congregate in human-altered coastal habitats

Mitsuhashi et al. (2018): urban raccoon dogs (*Nyctereutes procyonoides*) have a smaller HR than rural ones

Cronk and Pillay (2021): yellow mongoose (*Cynictis penicillata*) in urban regions have smaller HRs

Yu et al. (2022): rat snakes move to artificial structures for better prey availability and better thermoregulation

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).

Teitelbaum and Mueller (2019):

- **Nomadic movement:** movement with irregular timing and/or direction that produces both within- and between-year variability in location and movement patterns
- “Data from recent developments in animal tracking technology (e.g., longer-lasting and lighter GPS devices) show that species previously considered migrants or range residents can show irregular, often long-distance, movement patterns (flexible foraging movements of leatherback turtles across the north Atlantic ocean, To migrate, stay put, or wander Varied movement strategies in bald eagles, Big data analyses reveal patterns and drivers of the movements of southern elephant seals)”

## Effects of $\mathbb{E}(R)$

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, changes in physiology or behavior, physiological 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 (Harvey and Clutton-Brock

1981; ref?). 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; 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, and nomadism) are more likely to occur over evolutionary timescales

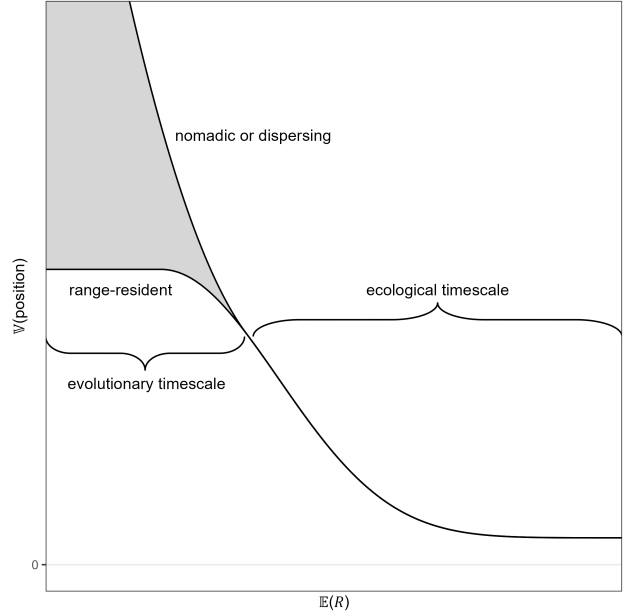


Figure 1: Hypothesized spatial needs (indicated as positional variance,  $\mathbb{V}(\text{position})$ ) of an animal as a function of mean resource abundance ( $\mathbb{E}(R)$ ). We expect low values of  $\mathbb{E}(R)$  to result in high  $\mathbb{V}(\text{position})$  as animals are forced to explore 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  $\mathbb{E}(R)$ .

rather than an animal’s lifespan (figure 1). 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 assumes the effect to be linear).

Animals living in large groups will often require larger home ranges because they will have to share resources with conspecifics (Prox and Farine 2020), but 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 HR (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,  $\tau_p$ ). As the amount of space an animal uses over its lifespan, the amount of time required to cross the area ( $\tau_p$ ) will also increase, so animals with  $\tau_p$  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 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

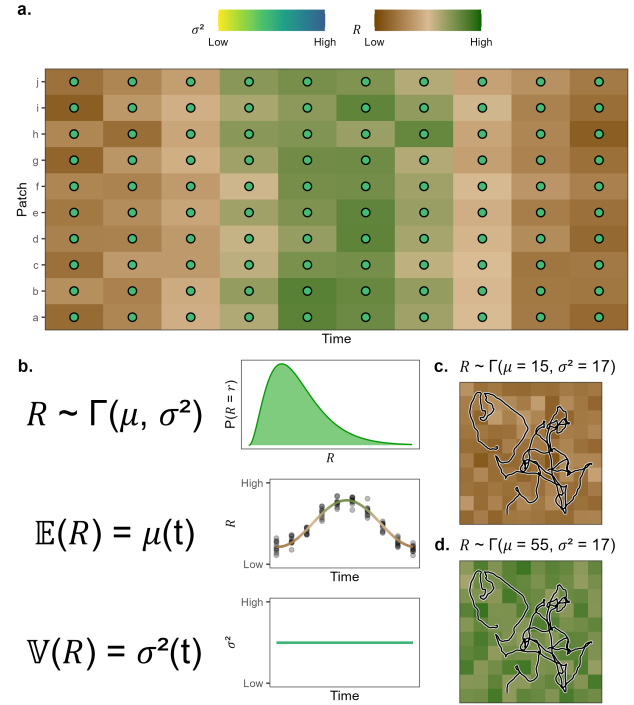


Figure 2: Fictitious example of variation in resource abundance in a heterogeneous environment with constant variance (after accounting for changes in mean abundance). (a.) Although resource abundance ( $R$ , raster fill) varies over time and space, the overall amount of variance (dot color) remains constant. (b.) Arbitrary definition of  $R$  as following a Gamma distribution with mean  $\mu$  and variance  $\sigma^2$ . (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  $\mathbb{V}(R)$ .

stochastic events (IPCC 2018; Noonan et al. 2018). Additionally, anthropogenic 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).

- Berger et al. (2018) fitness decreases with resources scarcity and lower temperatures

## Effects of $\mathbb{V}(R)$

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 the arrival of new competitors, fires, floods, droughts, and changes in climate (IPCC 2018; Noonan et al. 2018; Jolly 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 (refs?). 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. There thus remains a need for developing a more complete understanding of how animals’ spatial needs change with environmental stochasticity.

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). 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, torpor, and hibernation).

When the (un)predictability in  $R$  changes over time (figure 4a), changes in  $\mathbb{V}(R)$  may

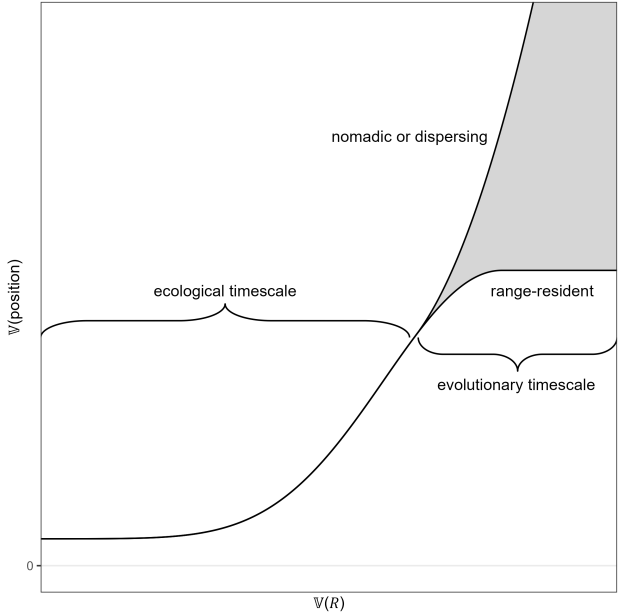


Figure 3: Hypothesized spatial needs (indicated as positional variance,  $\mathbb{V}(\text{position})$ ) of an animal as a function of resource unpredictability ( $\mathbb{V}(R)$ ). We expect low values of  $\mathbb{V}(R)$  to result in low  $\mathbb{V}(\text{position})$  as animals are able to depend on somewhat predictable resources. As  $\mathbb{V}(R)$  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  $\mathbb{V}(R)$  and  $\mathbb{V}(\text{position})$  cannot be linear because it would require  $\mathbb{V}(\text{position})$  to be negative for low values of  $\mathbb{V}(R)$ .

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 the expected  $R$  and its unpredictability 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  $\mathbb{V}(R)$ , since periods of high productivity can often be more variable than times of dormancy or lower productivity, and the variability in  $R$  can often change both within and between years. In highly variable and stochastic environments, animals will likely have higher spatial needs, particularly if they are required to collect and store resources for periods of scarcity or increased energetic needs. These include reproductive periods, whether this be due to pregnancy (ref?), to feed offspring (ref?), or because the animal's needs change over time (e.g., male deer growing antlers: French et al. 1956; Smolko et al.

2022). Thus, failing to account for changes in  $\mathbb{V}(R)$  can result in serious underestimations of animals' spatial needs, which may lead to decreases in population fitness and size while also increasing the risk of population collapse and human-wildlife conflict (Mukenka et al. 2019).

Extreme events (Logares and Nuñez 2012; Anderson et al. 2017) such as heat domes, 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

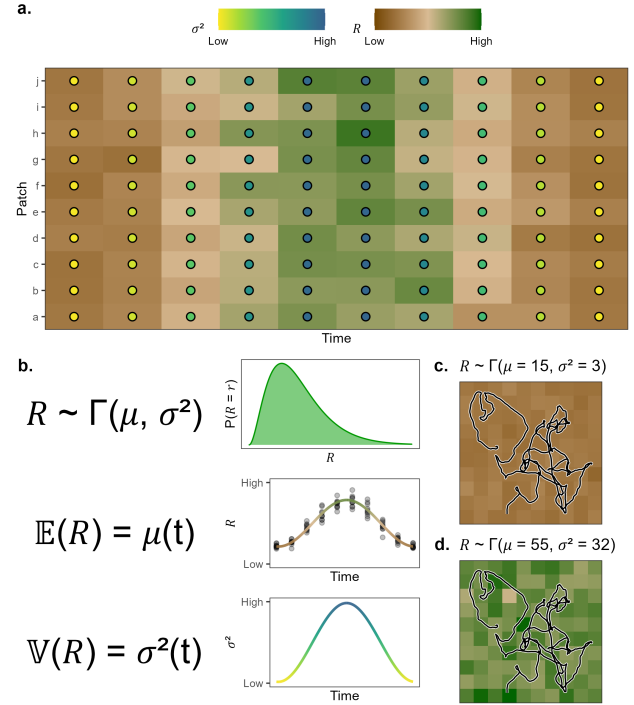


Figure 4: Fictitious example of variation in resource abundance in a heterogeneous environment with changing variance (even after accounting for changes in mean abundance). (a.) Although resource abundance ( $R$ , brown-green fill) varies over time and space, variance (dot color) is lowest at the beginning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

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; Amezcua 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).

The effects of  $\mathbb{V}(R)$  on animals' spatial requirements most likely vary between species, since different species have different energetic and nutritional needs (Boratyński 2020; Noonan et al. 2020), so the degree to which  $R$  varies will likely affect each species differently. Small-scale variations may be sufficient to cause changes in behavior for some small animals, while animals with larger spatial needs may not detect such differences. Rizzuto et al. (2021) found that the 50%, 75%, and 90% utilization distributions (UDs) of snowshoe hares (*Lepus americanus*) increased with average C:N in lowbush blueberry as well as the coefficient of variation for C:N, which suggests that the hares expanded their home range in response to both resource scarcity and the variance in resource scarcity. Similarly, Mueller et al. (2011) demonstrated that ungulate species in more variable ecosystems move more than species in more stable landscapes and that they are more likely to be nomadic. In contrast, Lucherini and Lovari (1996) found that red foxes (*Vulpes vulpes*) living in areas with more habitats per hectare (i.e., 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 of Canadian lynx (*Lynx canadensis*) decreased with seasonality. A subsequent analysis by Nilsen et al. (2005) found that various carnivores respond to resource variability and seasonality (albeit in contrasting ways) using the Canadian lynx data of Herfindal et al. (2005) along with data on wolverines (*Gulo gulo*), bobcats (*Lynx rufus*), and coyotes (*Canis latrans*). Additionally, 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  $\mathbb{E}(R)$ , so it is not only important to account for both  $e(R)$  and  $\mathbb{V}(R)$  but also interaction

effects between the two. It is 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 (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  $\mathbb{V}(R)$  is likely to have less of an effect if resources are always abundant, albeit unpredictable. Thus, we expect  $\mathbb{V}(R)$  to have a stronger effect on resource abundance when  $\mathbb{E}(R)$  is low, and less of an effect when  $\mathbb{E}(R)$  is high.

Figure 5 illustrates the simulated average spatial requirements of an animal 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  $var(R)$  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. This is because when  $\mathbb{E}(R)$  is low, small additive changes in  $\mathbb{E}(R)$  (e.g., from 1 to 2) correspond to large multiplicative changes (i.e., 2 is twice as big as 1). Additionally, the 95% home range is more sensitive to changes in  $\mathbb{E}(R)$  than the core home range  $H_{50\%}$  because larger quantiles (e.g., 95% > 50%) are more sensitive to changes in the home range.

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

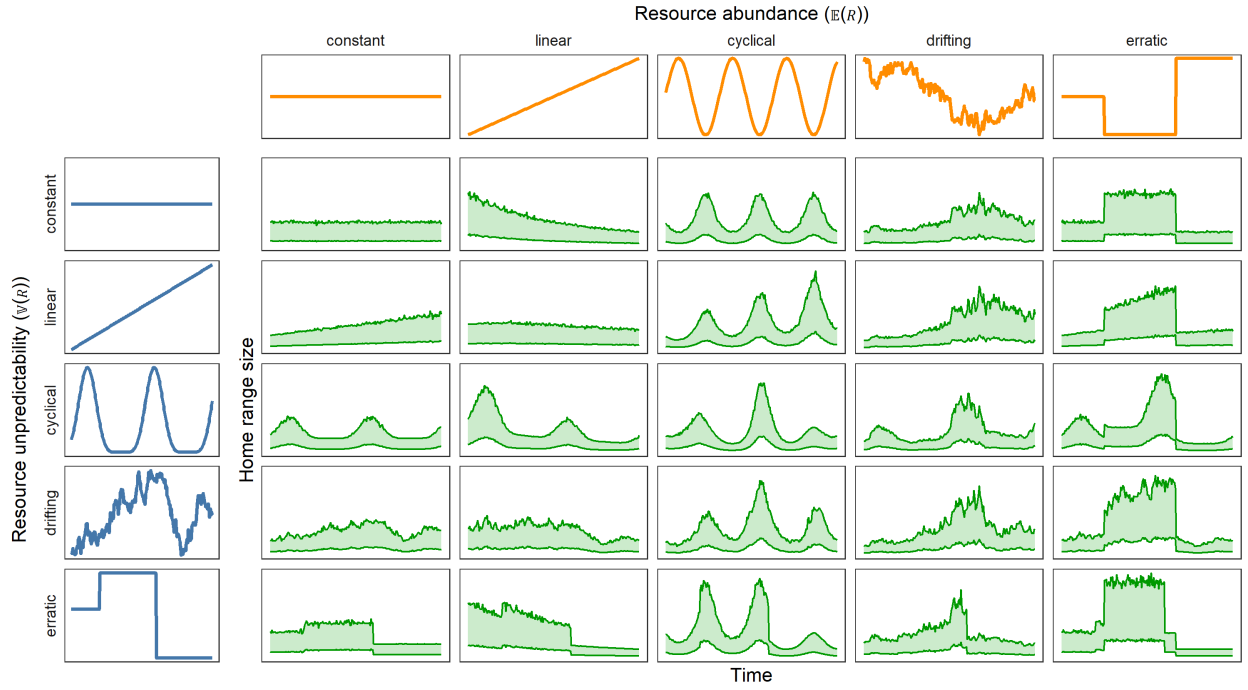


Figure 5: Simulated spatial requirements for animals living in habitats where the mean and variance in resource availability ( $R$ ) are constant, linearly increasing, cyclical, drifting, or erratic over time. The bottom line indicates the animal's core home range (0.5 quantile), while the top line indicates the 0.95 utilization quantile. Note how both quantiles decrease nonlinearly as  $\mathbb{E}(R)$  increases, and they increase approximately linearly 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 point  $\langle 0, 0 \rangle$  until they reach satiety, at which point they returned to  $\langle 0, 0 \rangle$  over the same amount of time. The animal's spatial variance parameter was then calculated using an Ornstein-Uhlenbeck Foraging (OUF) model via the `ctmm` package

closures). However, estimates of spatial requirements based on estimated changes in  $\mathbb{E}(R)$  should be interpreted carefully, since model error and unpredictable decreases in  $\mathbb{E}(R)$  (such as following fires) may increase animals' spatial needs 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 home range 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 the estimated home range size and the noise in the estimate increase with  $\mathbb{V}(R)$  (e.g., constant  $\mathbb{E}(R)$ , linear  $\mathbb{V}(R)$ ). This is because as the habitat becomes more stochastic, the amount of space required to reach satiety also becomes increasingly unpredictable.

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 change monotonically, especially when the trends are linear. 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 visible change in  $H_{50\%}$ . However, when  $\mathbb{E}(R)$  changes nonlinearly, it is easy to see how the increase in  $\mathbb{V}(R)$  amplifies the effects of  $\mathbb{E}(R)$ . 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  $\mathbb{V}(R)$ , and 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 (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 for mining purposes with a subsequent artificial re-forestation). However, if changes are stochastic but sufficiently small and frequent, animals may perceive them as few smooth changes rather a series of small, sudden, changes. Estimating trends in  $\mathbb{E}(R)$  and  $\mathbb{V}(R)$  requires a high cognitive capacity, since distinguishing between  $\mathbb{V}(R)$  and changes in  $\mathbb{E}(R)$  is not easy (Steixner-Kumar and Gläscher 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, the 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 resource abundance and stochasticity have on an-

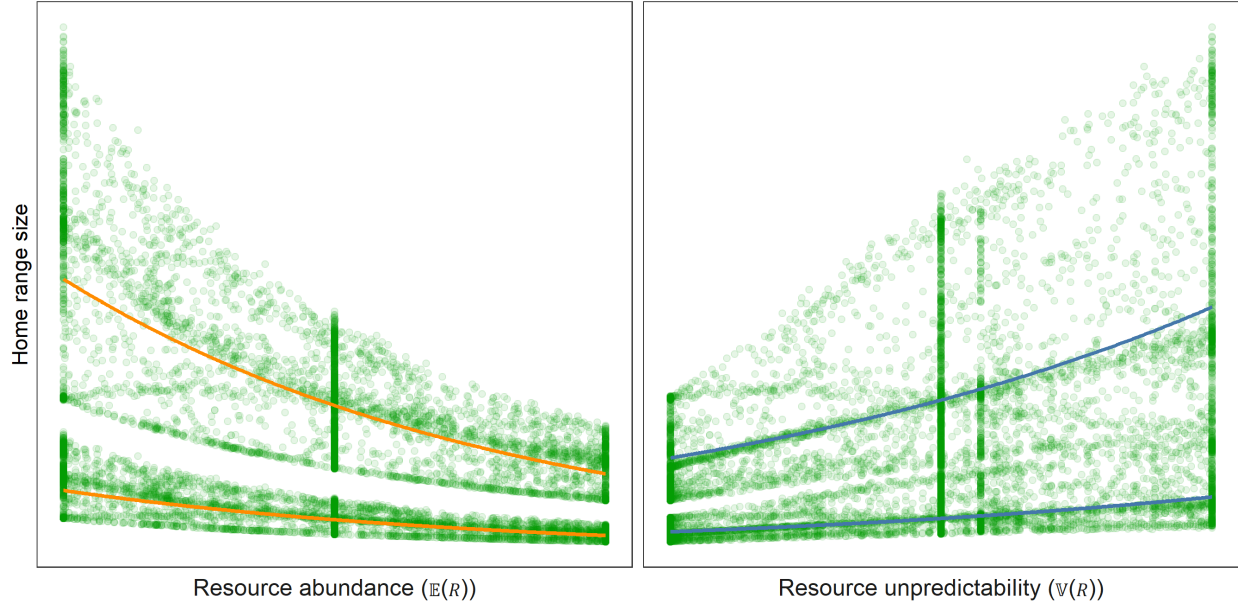


Figure 6: Effects of  $\mathbb{E}(R)$  and  $\mathbb{V}(R)$  on simulated spatial requirements. The relationships were estimated using a Generalized Linear Model with a Gamma family of distributions that accounted for the effects of both  $\mathbb{E}(R)$  and  $\mathbb{V}(R)$  as well as differences 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.

imals’ 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 once thought to have markedly different behaviors and spatial needs may instead have a single common functional response but different levels of  $\mathbb{E}(R)$  and  $\mathbb{V}(R)$  (**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 and we also provide 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 develop or memory about the frequency and severity of such events (elephants: Foley et al. 2008; Polansky et al. 2015). However, 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 and genetic diversity through the production of numerous offspring (**examples?**). Frequent and repetitive events may result in changes in animal behavior and memory (framework: Riotte-Lambert and Matthiopoulos 2020; elephants: Foley et al. 2008; bison and mule deer: Geremia et al. 2019; elk: Falcón-Cortés et al. 2021), while events that occur over larger spatiotemporal scales are more likely to promote slower changes through adaptation, natural selection, and evolution (Gienapp et al. 2008; Logares and Nuñez 2012; Anderson et al. 2017; Grant et al. 2017).

Events occur which multiple times at relatively predictable intervals during an animal’s lifespan and over multiple generations, such as the alternating of seasons, allow it 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) or caching resources (Post et al. 2006). Of course, an animal with a life span shorter than a year will be unable to

perceive the cyclical alternating of the seasons, and an animal with a life span 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 at least one or more years, 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 torpor (marmots: Inouye et al. 2000; ground squirrels: Goldberg and Conway 2021); and 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; 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).

Adaptability and responsiveness to change are strong determinants to whether an animal survives in a changing environment (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, yellow-bellied marmots (\*\*) []

Likewise, ungulates’ ability to time their yearly migrations on cues such as available forage biomass, hunting pressure, snow fall, and snow melt 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 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 cues 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; Buntgen 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, such as species that either fail to adapt (i.e., do not also shift) or species that are unable shift. Specialists and obligate symbionts are less likely to shift since their range is determined by their food sources' or 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 for commonalities and differences in the behaviors between members of the same population or species, as well as between multiple distinct populations or species.

Ecologists often conclude that populations from different regions behave differently (**examples?**), but the differences in behavior may only be due to differences in  $\mathbb{E}(r)$  or  $\mathbb{V}(R)$ , instead, which would cause animals to behave differently even if they depend on the same functional responses.

We start by providing examples and considerations on how one may model  $R$  to estimate  $\mathbb{E}(R)$  and  $\mathbb{V}(R)$ , animals' spatial needs, and the effects of  $\mathbb{E}(R)$  and  $\mathbb{V}(R)$  on animal's 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) are a class of statistical models that us to estimate changes in  $\mathbb{E}(R)$  and  $\mathbb{V}(R)$  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) for location and scale (GAMLSs). Currently, the `mgcv` package allows one to fit location-scale models with a variety distribution families, including Gaussian, scaled t, Gamma, Tweedie, Gumbel families.

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, 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, including elemental compositions (e.g., carbon to nitrogen ratio), total biomass (e.g., kg of carbon per m<sup>2</sup>), 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 not monotonic, we suggest using a GAM rather than a GLM. However, the complexity of the spatio-temporal terms should be chosen carefully, particularly the terms for the mean (i.e., location). Excessively wiggly mean terms will cause the variance to be underestimated and under-fit, and an excessively smooth mean terms will inflate the variance term, so an improperly defined model can lead to 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, REstricted Marginal Likelihood (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.

## 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). Since all models that can

be currently fit via the `ctmm` package (*Ctmm* n.d.) assume the animal to be range-resident and move with a single, consistent behavior, we suggest estimating an animal’s spatial needs using a **sliding window** approach.

**here**

Let  $w$  indicate a fixed window width.

In either case, the accuracy of the estimated parameters will depend strongly on the length of the observation period as well as the measurement frequency (Noonan et al. 2019*b*). 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. However, when an animal’s spatial needs change over time, models which assume range residency are not appropriate. Instead, a sliding window approach that estimates the short-term (e.g., weekly or monthly) spatial needs may produce sensible results. Modeling animal movement as an autocorrelated stochastic process is particularly useful in this approach, since it accounts the uncertainty and limited amount of information in short periods of tracking data (by accounting for difference in sample size and effective sample size – see Noonan et al. 2019*b*, 2019*a*).

## Modeling the relationships

Any linear model, including ANOVA-like models, would assume spatial needs can span all (complex) numbers, including negative values. Since spatial needs are strictly greater than zero, models that allow non-linear relationships while forcing the spatial needs to be strictly greater than zero.

- Gamma distribution for HR
- possibly location-scale if enough data?



## An empirical example: Lowland tapir in the Brazilian Cerrado

Animal's spatial needs are often estimated using all available tracking data. Doing so maximizes the (effective) sample size, but it also assumes that during the tracking period the animal's movement behavior did not change and that its home range did not shift either. Although these assumptions may be valid for relatively short tracking periods (and often necessary for reasonable estimates of spatial needs), few animals will behave consistently during the tracking period and use the same space every day. ***Most animals (if not all) use their space selectively.*** add examples with humans moving to different regions?

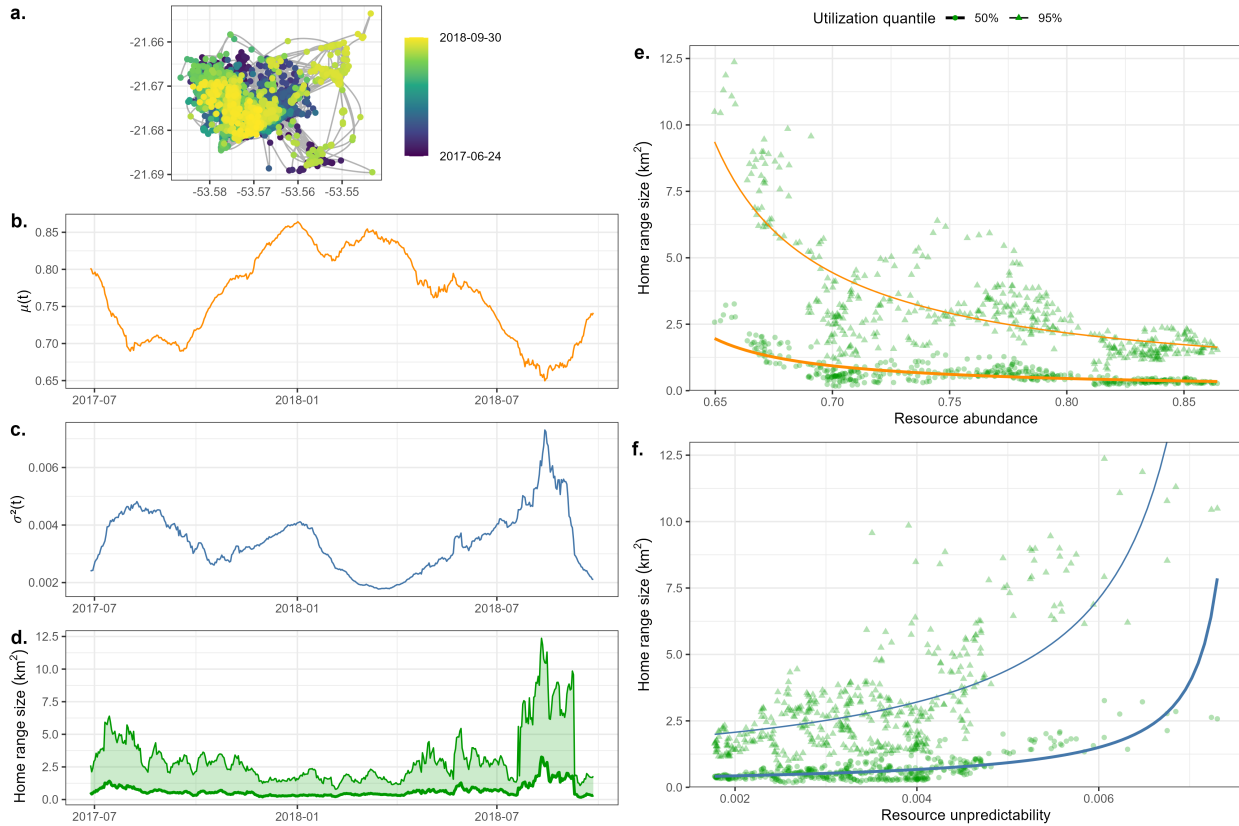


Figure 7: Seven-day home range size of a tapir (*Tapirus terrestris*) in response to changes in mean and variance in resource abundance. (a.) GPS tracking data of the tapir. (b.) Mean resource abundance estimated as the mean NDVI at the locations visited by the tapir. (c.) Variance in resource abundance 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% (bold) and 95% (thin) 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. The tapir movement data corresponds to the individual named "Anna" from the Cerrado sample of Medici *et al.* (2022).

Additional info is in appendix 2

we use NDVI (ref?) as a proxy for resource abundance.

## Using this framework in conservation-related decisions

text

- maps of resource abundance and resource unpredictability
- predict animal home range sizes for different levels of  $\mathbb{E}(R)$  and  $\mathbb{V}(R)$ ; pick stable areas (flatter parts of the curves)

## 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  $\mathbb{E}(R)$  and  $\mathbb{V}(R)$ , and we demonstrate the importance of accounting for  $\mathbb{V}(R)$  besides  $\mathbb{E}(R)$ . We also provide a framework for modeling animal behavior and movement continuously rather than imposing arbitrary thresholds between range-resident and nomadic animals. (notes on seasons and “seasonal behavior”)

## MISC

Other empirical refs to possibly add: Lindstedt and Boyce (1985), Jonzén et al. (2006), Wolkovich et al. (2012), Falcón-Cortés et al. (2021), Nathan et al. (2022)

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

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.

competition can promote niche partitioning (Fox 1981)

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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