

How resource abundance and stochasticity affect organisms' space-use requirements

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1 Abstract

2 The amount of space organisms use is thought to be tightly linked to the availability of
3 resources within their habitats, such that organisms living in productive habitats generally
4 require less space than those in resource-poor habitats. This hypothesis has widespread em-
5 pirical support, but existing studies have focused primarily on responses to the mean amount
6 of resources, while responses to the variance around the mean are still largely unknown. This
7 is not a trivial oversight. Organisms adjust to variable environmental conditions, so failing
8 to consider the effects of resource (un)predictability can result in a limited understanding
9 of organisms' space-use requirements, challenging ecological theory and applied conservation
10 alike. In this study, we leverage the available literature to provide a unifying framework and
11 hypotheses for the effect of mean and variance in resources on organisms' space use. Next,
12 we use simulated movement data to demonstrate how the combined effects of mean and
13 variance in resource abundance interact to shape predictable patterns in space use. Finally,
14 we use real-world tracking data on a lowland tapir (*Tapirus terrestris*) from the Brazilian
15 Cerrado to show how this framework can be applied to better understand the movement
16 ecology of free-ranging animals.

¹⁷ **Introduction**

¹⁸ The amount of resources an organism is able to access is a strong determinant of its odds
¹⁹ of survival and reproduction. Resource limitations can cause individuals to experience a
²⁰ negative energetic balance, which can then result in lower fitness (Le Bot et al. 2019; Hou
²¹ et al. 2020), altered physiology (Wessling et al. 2018; Le Bot et al. 2019; Rocha et al. 2021;
²² Dai Pra et al. 2022), lower chance of reproduction (Douglas and Pearce-Higgins 2014; Le
²³ Bot et al. 2019; Schmidt et al. 2020; Stefanescu et al. 2021), and even death (Foley et
²⁴ al. 2008; Berger et al. 2018), along with changes to community structure (Burson et al.
²⁵ 2018; Ghislandi et al. 2018; Haney and Siepielski 2018; Riotte-Lambert and Matthiopoulos
²⁶ 2020). Thus, many organisms adapt their behaviors in response to changes in local resource
²⁷ abundance to ensure their needs are met. Movement represents one of the most readily
²⁸ available behaviors that species can adjust to optimize their resource use (Charnov 1976;
²⁹ Kacelnik et al. 1992).

³⁰ The relationship between organisms' movement and resource abundance has been of
³¹ interest to biologists for nearly a century. Burt (1943) considered the search for food as
³² the primary driver for movement within an organism's home range. Three decades after,
³³ Southwood (1977) suggested that change in resource abundance is a strong determinant of
³⁴ how organisms decide where to live and when to reproduce. Two years later, Harestad and
³⁵ Bunnel (1979) proposed that the simplest relationship between resource abundance and an
³⁶ organism's home-range size is

$$H = C/R, \quad (1)$$

³⁷ where H is the organism's home-range size, C is the organism's resource consumption (kcal
³⁸ day^{-1}), and R is the resources the organism can access ($\text{kcal day}^{-1} \text{ unit area}^{-1}$). Harestad
³⁹ and Bunnel's model is simple to conceptualize and allows for testable predictions, but it fails
⁴⁰ to account for the nonlinear relationship required to avoid negative home range estimates

41 (e.g., fig. 2 in the work of Bista et al. 2022). Many researchers have since demonstrated that
42 organisms adapt their home ranges in response to resources abundance, but studies often fail
43 to build upon previous work. Instead, results are typically reported as independent, novel
44 findings. Thus, there remains a need for a clear hypothesis for the effects of resource abun-
45 dance on organisms' space-use requirements. Additionally, while much work has been done
46 on estimating organisms' responses to average resource abundance, there is little information
47 on how they respond to unpredictable changes in resources (but see: Stephens and Charnov
48 1982; Rizzuto et al. 2021).

49 Here, we refer to a location's average amount of resources as "resource abundance",
50 while we use the phrase "resource stochasticity" to indicate the variability in resources after
51 accounting for changes in the mean. We argue that, on its own, a habitat's long-term resource
52 abundance is not sufficient to assess the habitat's quality, nor make predictions about how
53 much space an organism might use. For instance, herbivores in a grassland with relatively
54 low but constant forage availability (low mean and variance) will adopt different behaviors
55 and adaptations from herbivores in a desert with equally scarce forage but rare, sudden, and
56 strong pulses of resources (low mean and high stochasticity). In the grassland, an animal
57 may require a large but constant home range as it moves between locations in search of food
58 (Teitelbaum and Mueller 2019), while an animal in the desert may switch between dispersal
59 in search for high-resource patches and short-term range residency whinith patches (Charnov
60 1976). Although it may be possible for both habitats to have the same long-term average
61 resource abundance, the differences in resource unpredictability result in different selection of
62 movement and life history strategies. Although resource unpredictability (and seasonality)
63 may ecrease organisms' fitness and a landscape's energetic balance (Chevin et al. 2010),
64 there is still limited empirical evidence to support this hypothesis (but see: Herfindal et al.
65 2005; Nilsen et al. 2005; Rizzuto et al. 2021).

66 Here, we illustrate how organisms' space use depends on both the abundance and unpre-
67 dictability of resources. First, we set the theoretical background necessary for the successive

68 sections by introducing key concepts and notation. Next, we provide a review of the effects
69 of resource abundance on organisms' space use while suggesting a unifying hypothesis. Af-
70 terwards, we provide a review of the effects of resource stochasticity on organisms' space use
71 while suggesting a second unifying hypothesis. Subsequently, we demonstrate the power of
72 these two hypotheses using quantitative, simulated responses to changes in resource abun-
73 dance and unpredictability. Finally, we demonstrate how this framework can be used in
74 practice to describe the movement ecology of a lowland tapir (*Tapirus terrestris*) from the
75 Brazilian Cerrado (Medici et al. 2022). Results from the simulations and empirical example
76 are presented using a fully transparent approach that allows researchers to replicate the work
77 and apply the methods to their own tracking data.

78 Resources as a random variable

79 Resources are often unpredictable (and difficult to quantify), since they depend on various
80 factors which cannot be accounted for easily, including climate (Lindstedt and Boyce 1985;
81 Morellet et al. 2013; Schmidt et al. 2020), weather (Morellet et al. 2013; Fjelldal et al.
82 2021), competitive pressure (Rich et al. 2012; Tórrez-Herrera et al. 2020), and differences
83 in energetics at the individual (Schmidt et al. 2020) and species level (Jetz et al. 2004).
84 Thus, let the random variable R indicate the amount of resources at a given point in space
85 and time. Quantifying resources as a numerical random variable, as opposed to using *ad hoc*
86 qualitative descriptions, provides us with the capacity to leverage techniques from probability
87 theory and statistics. We assume readers are familiar with fundamental statistical concepts
88 (e.g., random variables, probability distributions, expected value and variance of a random
89 variable), but we define and explain the necessary concepts in Appendix A.

90 Effects of resource abundance, $E(R)$

91 While organisms' needs vary greatly between taxonomic groups, some needs are essential
92 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 can 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 (Charnov 1976; Brown et al. 1999), but they must also account for a higher metabolism and movement costs (Taylor et al. 1982). The hypothesis that space-use requirements decrease with resource abundance, $E(R)$, is commonly accepted and well supported, but many studies assume a linear relationship (e.g., Harestad and Bunnel 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 a linear relationship can lead to questionable estimates and problematic biases, such as negative or excessively small home ranges (e.g., fig. 2 in the work of Bista et al. 2022). Conceptually, the relationship between space-use requirements and $E(R)$ must be nonlinear, since there are limits to how much space an organism is able to explore in its lifetime and a minimum amount of space it requires to survive (which is necessarily greater than zero – see: Lucherini and Lovari 1996; Herfindal et al. 2005; Nilsen et al. 2005; Simcharoen et al. 2014; Watson 2020, and contrast them to the estimates based on linear models listed above).

Fig. 1 illustrates our first of two hypotheses: When $E(R)$ is high, we expect organisms' spatial requirements to be relatively small and near the smallest amount of space required to survive (e.g., Relyea et al. 2000; Herfindal et al. 2005; Nilsen et al. 2005). At lower values of $E(R)$, we expect organisms' spatial requirements to increase nonlinearly, since low values of $E(R)$ force organisms to expand their home ranges (Lucherini and Lovari 1996; 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). It is unclear when organisms switch from range residency to migration or nomadism (or vice-versa), but understanding the connection between these

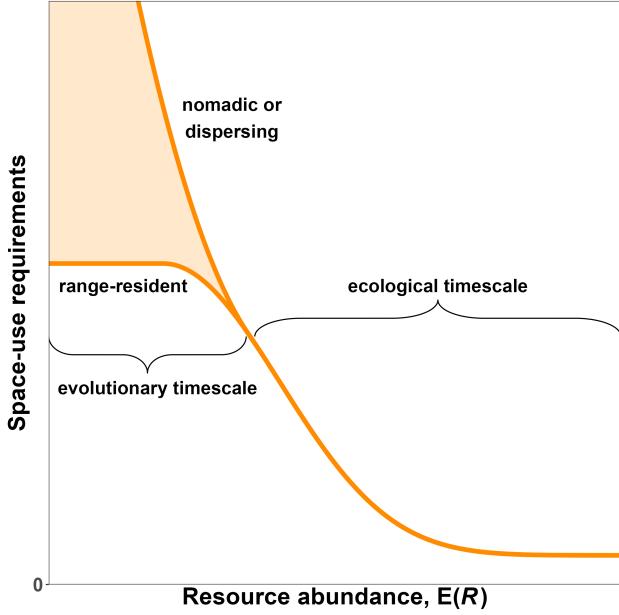


Figure 1: Hypothesized space-use requirements of an organism as a function of resource abundance ($E(R)$). We expect low values of $E(R)$ to result in high space-use requirements as organisms are forced to explore large areas to collect the resources they require to survive, whether they be range-resident or nomadic. As $E(R)$ increases, space-use requirements should decrease nonlinearly until they reach the minimum amount of space required by the organism to survive. Note that the relationship between $E(R)$ and space-use requirements cannot be linear because it would require space-use requirements to be negative for high values of $E(R)$.

types of movement is important for quantifying the effect of resource abundance on organisms' space-use requirements and when an organism may choose to migrate or disperse rather than remaining range-resident (mammals: Teitelbaum et al. 2015; moose, *Alces alces*: Singh et al. 2012; eagles, *Haliaeetus leucocephalus*: Wheat et al. 2017; Poessel et al. 2022; lesser flamingos, *Phoeniconaias minor*: Pretorius et al. 2020). Still, species-level changes in movement behavior are more likely to occur over evolutionary timescales than over an organism's lifespan, since larger ranges require greater vagility, which, in turn, is facilitated by morphological features such as hinged joints and elongated limbs (Andersson 2004; Jetz et al. 2004; Samuels et al. 2013; Hirt et al. 2017).

Consider the scenario where $E(R) = \mu(t)$ changes over time but $\text{Var}(R) = \sigma^2 > 0$ is constant over time and space (fig. A1). Since R is random, an organism that moves in the landscape will not find the same R at different time points or throughout the habitat. However, if $\mu(t)$ changes repetitively and regularly over time (e.g. peaks each spring and is

¹³³ lowest in winter), an organism may learn to predict times of high or low $E(R)$ (Samarra et
¹³⁴ al. 2017; Abrahms et al. 2019; Geremia et al. 2019; e.g., Falcón-Cortés et al. 2021) but will
¹³⁵ still not be able to predict R exactly.

¹³⁶ **Effects of resource stochasticity, $\text{Var}(R)$**

¹³⁷ The example illustrated in the section above can occasionally be a useful simplification of
¹³⁸ relatively stable environments or when data is scarce, but it likely not realistic, since $\text{Var}(R)$
¹³⁹ often also changes over time. Periods of scarcity (e.g., winter, droughts) not only have
¹⁴⁰ lower $E(R)$ but also have narrower ranges of R . In contrast, periods of high $E(R)$ (e.g.,
¹⁴¹ spring green-up) also often tend to have higher $\text{Var}(R)$ because R tends to vary across wider
¹⁴² ranges (e.g., due to high spatial variability, or high R followed by low R after grazing).
¹⁴³ When both $E(R)$ and $\text{Var}(R)$ change over time (fig. A2), predicting R becomes more com-
¹⁴⁴ plex, since disentangling changes in $E(R)$ and $\text{Var}(R)$ is not simple (Steixner-Kumar and
¹⁴⁵ Gläscher 2020). Statistically, this is because the more change one attributes to $\mu(t)$ (i.e.,
¹⁴⁶ the wigglier it is), the smaller $\sigma^2(t)$ becomes. Conversely, the smoother $\mu(t)$ is, the larger
¹⁴⁷ $\sigma^2(t)$ becomes. Biologically, this is important because an organism's perception scale (Levin
¹⁴⁸ 1992) determines whether it sees a change in R as a trend in $E(R)$ or as a stochastic event
¹⁴⁹ (i.e., due to $\text{Var}(R)$). An organism's perception of changes in R will also depend strongly
¹⁵⁰ on its cognitive capacities and memory (Foley et al. 2008; Fagan et al. 2013; Mueller et
¹⁵¹ al. 2013; Abrahms et al. 2019; Falcón-Cortés et al. 2021). Whether, an organism is able to
¹⁵² predict trends in $\sigma^2(t)$ or not, environmental variability is thought to reduce a landscape's
¹⁵³ energetic balance (Chevin et al. 2010), which, in turn, decreases organisms' fitness (e.g.,
¹⁵⁴ Berger et al. 2018) and increases their space-use requirements. While this is true for both
¹⁵⁵ predictable and unpredictable stochasticity, extreme and rare events are more likely to have
¹⁵⁶ a stronger effect due to their unpredictability and magnitude (Logares and Nuñez 2012;
¹⁵⁷ Anderson et al. 2017). A few recent studies support these hypotheses (Chevin et al. 2010;
¹⁵⁸ Morellet et al. 2013; Nandintsetseg et al. 2019; Riotte-Lambert and Matthiopoulos 2020),

159 but many of them are limited in geographic and taxonomic scales, so the extent to which
160 these preliminary findings can be generalized is still limited. Thus, there remains a need for
161 developing a more complete understanding of how organisms' space-use requirements change
162 with environmental stochasticity.

163 Similarly to $E(R)$, we hypothesize $\text{Var}(R)$ to have a nonlinear effect on organisms' space-
164 use requirements. When $\text{Var}(R)$ is low enough that R is relatively predictable, we do not
165 expect changes in $\text{Var}(R)$ to have a noticeable effect. But as resources become increasingly
166 unpredictable, we expect space-use requirements to increase progressively faster (fig. 2) be-
167 cause: (1) as $\text{Var}(R)$ increases, the chances of finding low R increase superlinearly, (2)
168 stochastic environments tend to be less productive (Chevin et al. 2010), (3) stochasticity
169 reduces an organism's ability to specialize and reduce competition for R (Levins 1974), and
170 (4) the added movement required to search for food increases organisms' energetic require-
171 ments. If resources remain highly unpredictable over long periods of time (e.g., multiple
172 lifespans), organisms may evolve or develop new behaviors (such as nomadism, dispersal,
173 and migration) or adaptations (such as increased fat storage or food caching). If changes in
174 $\sigma^2(t)$ are sufficiently predictable, organisms may learn to anticipate and prepare for periods
175 of greater stochasticity by pre-emptively caching food, migrating, or relying on alternative
176 food sources during stochastic events (e.g., the seasonal arrival of competitors).

177 Interactive effects of $E(R)$ and $\text{Var}(R)$

178 We have provided the case for why both $E(R)$ and $\text{Var}(R)$ affect organisms' space-use require-
179 ments, but we presented the two parameters as independent drivers of movement. However,
180 organisms may respond to changes in $\text{Var}(R)$ more when resources are scarce than when they
181 are abundant. Consequently, models estimating the effects of R on organism's movement
182 should account for not only the marginal effects of $E(R)$ and $\text{Var}(R)$ but also their interac-
183 tive effects. A highly unpredictable habitat may be very inhospitable if resources are poor,
184 but $\text{Var}(R)$ may have little effect if resources are stochastic but always abundant. Thus, we

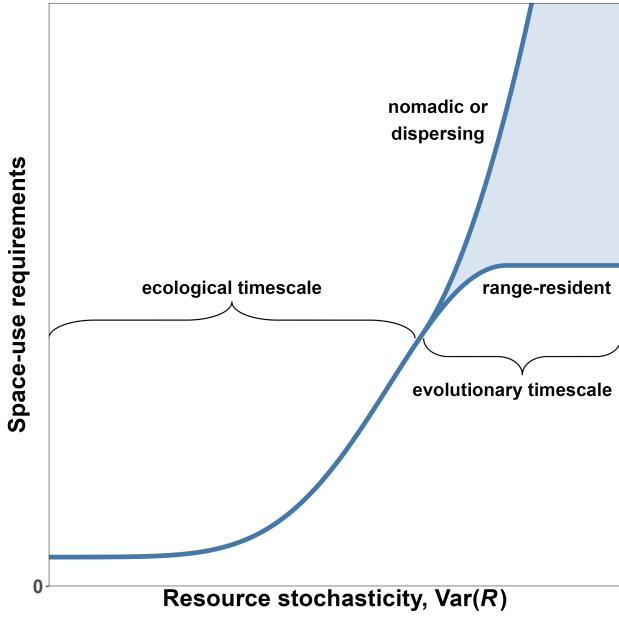


Figure 2: Hypothesized space-use requirements of an organism as a function of resource stochasticity ($\text{Var}(R)$). We expect low values of $\text{Var}(R)$ to result in low space-use requirements as organisms are able to depend on relatively predictable resources. As $\text{Var}(R)$ increases, space-use requirements should increase nonlinearly, whether this results in an expansion of the home range (in the case of range-resident organisms) or a switch to dispersal, nomadism, or migration. Note that the relationship between $\text{Var}(R)$ and space-use requirements cannot be linear because it would require space-use requirements to be negative for low values of $\text{Var}(R)$.

185 expect $\text{Var}(R)$ to have a stronger effect on space-use requirements when $E(R)$ is low, and
 186 less of an effect when $E(R)$ is high. We explore this more in the following section.

187 **Simulating responses to $E(R)$ and $\text{Var}(R)$**

188 To support our hypotheses of how organisms' space use is affected by $E(R)$, $\text{Var}(R)$, and the
 189 interaction effect of $E(R)$ and $\text{Var}(R)$, we present the results from a series of quantitative
 190 simulations. To start, we used the `ctmm` package (Fleming and Calabrese 2021) for `R` (`R`
 191 Core Team 2023) to generate 200 tracks (see Appendix B for sensitivity analyses) from an
 192 Integrated Ornstein-Uhlenbeck movement model (IOU model, see Gurarie et al. 2017). The
 193 IOU model's correlated velocity produces realistic tracks with directional persistence despite
 194 the tracks being discrete samples of continuous-time movement processes. However, unlike
 195 Ornstein-Uhlenbeck (OU) and Ornstein-Uhlenbeck Foraging (OUF) models, IOU models do
 196 not produce spatially stationary movement, so the organism is not range-resident. Con-

197 sequentially, each track is spatially unrestricted and can be interpreted as purely exploratory
198 movement.

199 Each of the 200 tracks were placed on a raster with common starting point $\langle 0, 0 \rangle$ and
200 sufficient time between tracks to be independent of one another (other than the starting
201 point). Each time the track moved to a new cell, the organism collected resources R sampled
202 from a Gamma distribution. The mean and variance of the distribution were defined by
203 deterministic functions $\mu(t)$ and $\sigma^2(t)$ (orange and blue lines in fig. 3). The value of t
204 was constant within each set of 200 tracks, so the time spent moving by the organism in
205 each track did not affect the distribution R was sampled from. Tracks were truncated once
206 the organism reached satiety, and the organism was given enough time to return to $\langle 0, 0 \rangle$
207 independently from the following track. Finally, as each set of 200 truncated was now
208 spatially restricted and centered around $\langle 0, 0 \rangle$, the set of tracks was modeled to calculate
209 the 95% utilization distribution from an OUF model and Autocorrelated Kernel Density
210 Estimate. We designed the simulations presented here to estimate the effects of $E(R)$ and
211 $\text{Var}(R)$ in simplistic environments. Consequently, we made the following four assumptions:
212 (1) $E(R)$ and $\text{Var}(R)$ are constant over space and short periods of time (i.e., within each set
213 of 200 tracks, but not over t). (2) Organisms move randomly in the environment with no
214 energetic costs. (3) Organisms have no perceptive range or memory, so they are unable to
215 detect, learn, or predict where resources are abundant (high $E(R)$) or reliable (low $\text{Var}(R)$)
216 over time. (4) Resources do not deplete, and there is no competition or predator avoidance.
217 Additional information is provided in Appendix B.

218 Fig. 3 shows how simulated space-use requirements responded to changes in $\mu(t)$ and
219 $\sigma^2(t)$ in scenarios where both functions can remain constant, increase linearly, oscillate
220 cyclically, drift stochastically, or change erratically. The top row shows how space-use re-
221 quirements vary for different trends in $\mu(t)$ while $\text{Var}(R)$ remains constant (like in fig. A1).
222 As $E(R)$ increases at a constant slope (linear $\mu(t)$) H decreases nonlinearly, with larger
223 changes when $E(R)$ is low, until it approaches the minimum size required by the organism.

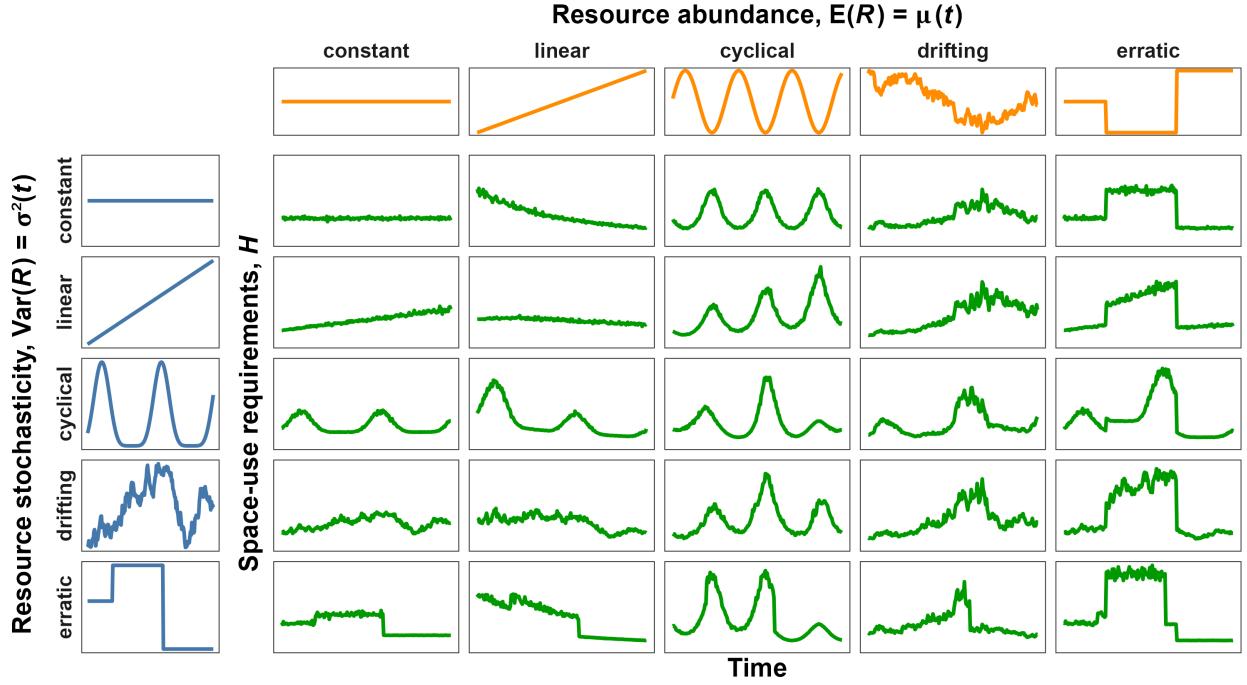


Figure 3: Simulated home range sizes, H , of an organism living in habitats where the mean and variance in resources are constant, linearly increasing, cyclical, drifting, or erratic over time (and homogenous over space). Note how H decreases nonlinearly as $\mu(t)$ increases and increases nonlinearily as $\sigma^2(t)$ increases. Additionally, the variance in H is higher when $\mu(t)$ is lower or $\sigma^2(t)$ is higher, and changes in $\sigma^2(t)$ have greater impacts when $\mu(t)$ is low.

224 Although less evident, note how the noise in the lines also decreases as $E(R)$ increases.

225 The leftmost column of fig. 3 illustrates the effects of $\text{Var}(R)$ on the simulated space-use
 226 requirements while $E(R)$ remains constant. Overall, both mean H and the variance around
 227 it increase with $\sigma^2(t)$ (most visible with constant $E(R)$ and linear $\text{Var}(R)$). This is because,
 228 similarly to resource-poor periods, times of greater stochasticity require the organism to
 229 move over larger areas for longer periods of time. This results in a greater uncertainty in
 230 how much time and space the organism will require to reach satiety, or indeed whether
 231 an organism living in highly stochastic environments can even reach satiety within a finite
 232 amount of time.

233 The remaining panels in fig. 3 illustrate $E(R)$ and $\text{Var}(R)$ jointly affect H and how
 234 complex the effects can be. Since $E(R)$ and $\text{Var}(R)$ have opposite effects on H , disentangling
 235 the effects can be particularly difficult when both parameters change in a correlated manner
 236 (e.g., linear $E(R)$ and $\text{Var}(R)$). When both $E(R)$ and $\text{Var}(R)$ increase linearly, H initially

increases since the effect of $\text{Var}(R)$ is stronger, but then decreases as the effect of $E(R)$ begins to dominate. Difficulties in disentangling the two effects are explored in greater depth in the case study in the following section.

Although the temporal trends in fig. 3 are complex and the effects of $E(R)$ and $\text{Var}(R)$ can be hard to disentangle, two simple relationships emerge when H is shown as a function of either $E(R)$ or $\text{Var}(R)$, rather than time (panels A and B of fig. 4). The estimated relationships follow the hypotheses we presented in figs. 1 and 2, although we found that the effect of $\text{Var}(R)$ at average $E(R)$ was linear with a slight sublinear saturation as $\text{Var}(R)$ increased. However, notice that the effect of $\text{Var}(R)$ on $E(H)$ depends strongly on $E(R)$ (panel C). The increase in $E(H)$ over $\text{Var}(R)$ is strongly nonlinear at low values of $E(R)$, but it is not affected by $\text{Var}(R)$ much when $E(R)$ is very low (and $E(H)$ is consequently very high).

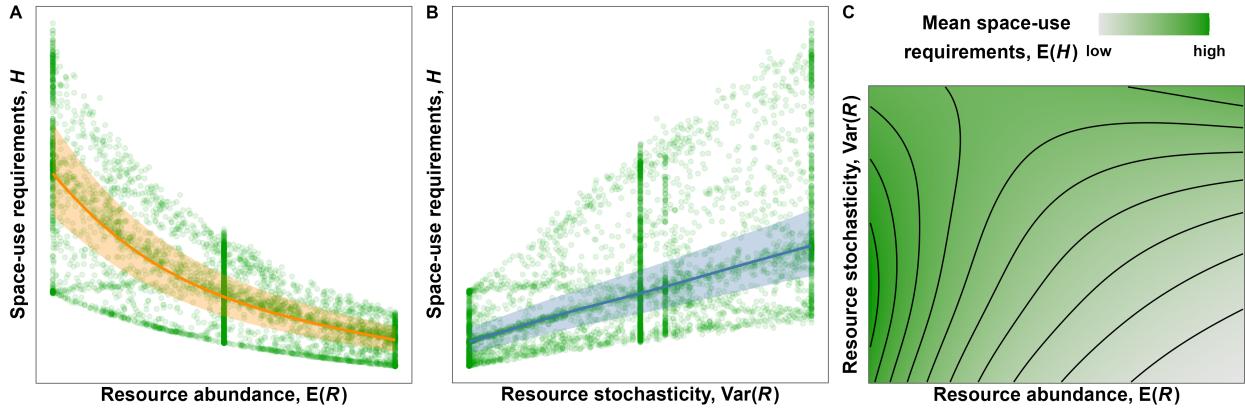


Figure 4: Effects of $E(R)$ and $\text{Var}(R)$ on simulated spatial requirements with 95% Bayesian credible intervals for the mean. While the effect of $\text{Var}(R)$ is sublinear in panel B, the effect of $\text{Var}(R)$ depends strongly on $E(R)$ (see panel C). Credible intervals were calculated using 10,000 samples from the posterior distribution. The relationships were estimated using a Generalized Additive Model for Location and Scale with a Gamma location-scale family of distributions (`mgcv::gammals`). Details on the model structure are provided in Appendix B.

As expected by the changes in the spread of the points in panels A and B of figure 4, the variance in H also depends on $E(R)$ and $\text{Var}(R)$ (figure 5A-B). Here, the effects of the two variables are more pronounced, even for low values of $E(R)$ or high values of $\text{Var}(R)$. Consequences of these effects are explored in the discussion section.

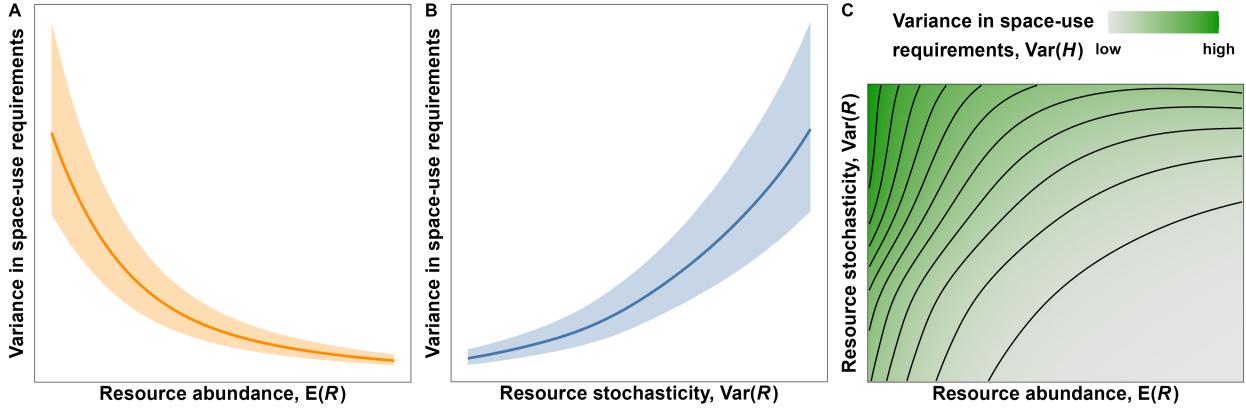


Figure 5: Effects of $E(R)$ and $Var(R)$ on the variance in simulated spatial requirements, with 95% Bayesian credible intervals for the estimated variance. Credible intervals were calculated using 10,000 samples from the posterior distribution. Additional details on the model structure are provided in Appendix B.

253 A case study on a lowland tapir in the Brazilian Cerrado

254 The simulations in the section above mostly follow the hypotheses we presented in the
 255 introduction, but they are based on assumptions that are often not met in real natural en-
 256 viroments. Organisms live in spatiotemporally heterogeneous and dynamic environments,
 257 which the development of perceptual ranges, navigation, and memory. Together, these abil-
 258 ities result in selective space use that depends on resource availability (Kacelnik et al. 1992)
 259 and resource depletion (Charnov 1976).

260 In this section, we test the hypotheses illustrated in the introduction using empirical
 261 tracking data on a lowland tapir from the Brazilian Cerrado along with estimates of $E(R)$ and
 262 $Var(R)$ using the Normalized Difference Vegetation Index (NDVI, see Pettorelli et al. 2011),
 263 a remote-sensed measure of landscape greenness, as a proxy of forage abundance. Appendix
 264 C contains additional information on how NDVI was modeled along with details on the
 265 continuous-time movement models (Noonan et al. 2019a; Fleming and Calabrese 2021) and
 266 autocorrelated kernel density estimation (Noonan et al. 2019b; Alston et al. 2022; Silva et
 267 al. 2022) used to quantify the tapir's space-use requirements. Through this example, we aim
 268 to provide support for the two hypotheses using empirical data that do not depend on as
 269 strong assumptions as those required by the simulations in the section above. Concurrently,

we also hope to show the potential complications that arise with empirical data.

Fig. 6 illustrates how a tapir in the Brazilian Cerrado (data from the individual labelled as “Anna” in the dataset from Medici et al. 2022) adapts its spatial needs to changes in $E(R)$ and $\text{Var}(R)$. Panels A and B show the changes in seven-day average mean and variance in NDVI, respectively, experienced by the tapir during the tracking period. The mean and variance in NDVI were estimated using a Generalized Additive Model for Location and Scale Bjorndahl et al. (2022) with a Beta family of distributions (NDVI values ranged from 0.3534 to 0.9475). Panel C shows the changes in the tapir’s 7-day home range over time. Note how the tapir uses more space during periods of lower NDVI (e.g., August 2017) and less space during periods with high NDVI (January 2018). Additionally, 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 (e.g., January 2018). Finally, panels D and E show the estimated (marginal) effects of $\mu(t)$ and $\sigma^2(t)$ on the tapir’s space use. Since $\mu(t)$ and $\sigma^2(t)$ are strongly correlated (panel F) and (spatio)temporally autocorrelated (panels A and B), the effects of R on H should be modeled carefully. To avoid over-fitting the model, we constrained the smooth effects of $\mu(t)$ and $\sigma^2(t)$ using a shape-constrained additive model (Pya 2022) with monotone decreasing and increasing P-splines for $\mu(t)$ and $\sigma^2(t)$, respectively. Additional information is provided in appendix C. Overall, the results presented in fig. 6 support our hypotheses, as the tapir’s 7-day home range decreases nonlinearly with $\mu(t)$ and increases nonlinearly with $\sigma^2(t)$. However, due to the strong nonlinear correlation between the two predictors, the marginal effects do not follow the data closely, particularly in the case of $\mu(t)$. We provide comments about these results in the related section in the discussion below.

Discussion

This paper presents two hypotheses for describing the effects of resource abundance and stochasticity on organisms’ space-use requirements. We support the hypotheses using quan-

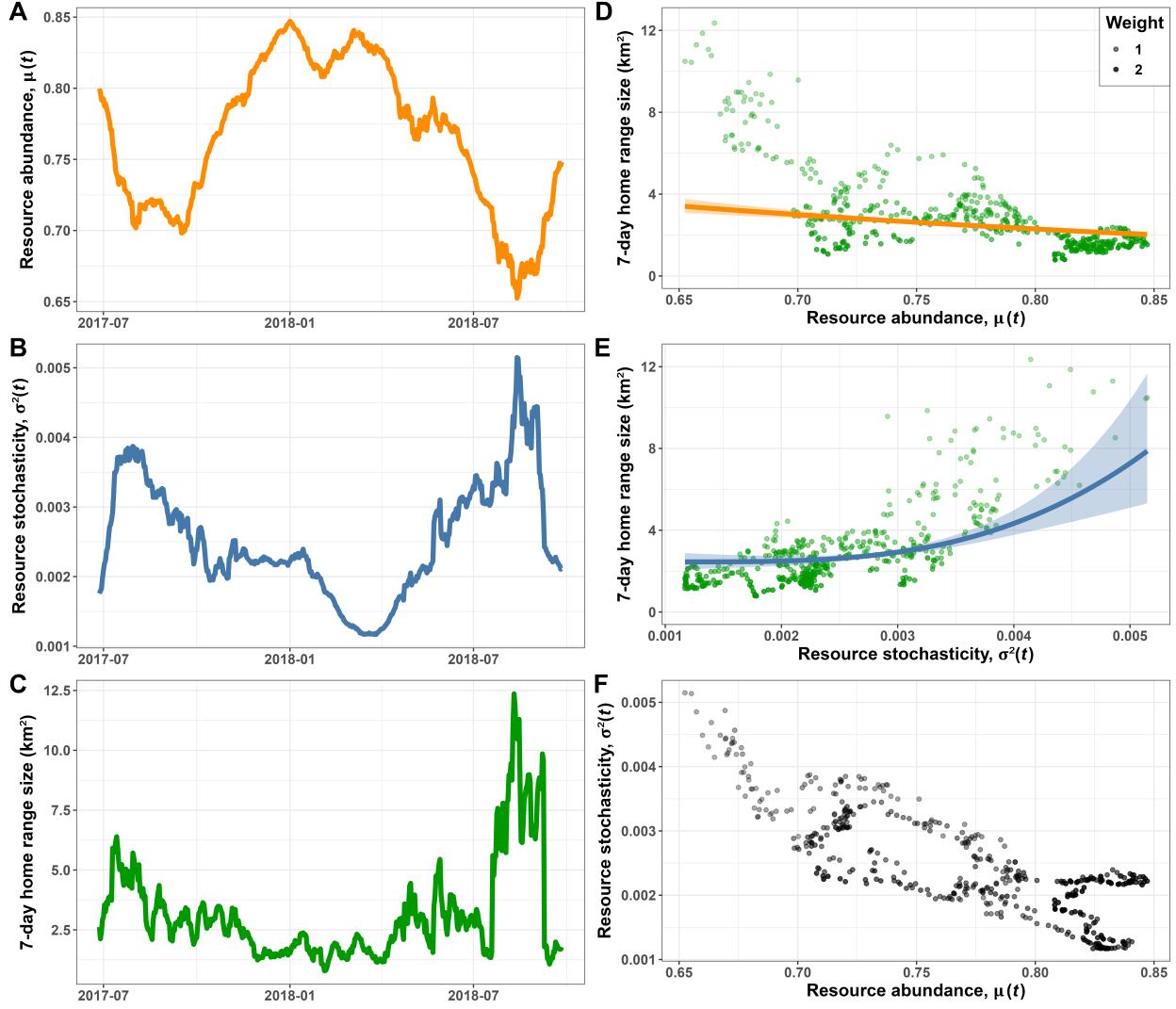


Figure 6: Seven-day home-range size of a lowland tapir (*Tapirus terrestris*) in response to changes in mean and variance in resources. (A) Trends in resource abundance over time, $\mu(t)$, estimated as the average mean NDVI at the locations visited by the tapir during a seven-day period. (B) Variance in resources over time, $\sigma^2(t)$, estimated as the average variance in NDVI at the locations visited by the tapir during a seven-day period. (C) Estimated seven-day home range based on the 95% utilization quantiles. (D, E) Estimated marginal effects of $\mu(t)$ and $\sigma^2(t)$ on home-range size. The model accounted for the marginal effects of $\mu(t)$ and $\sigma^2(t)$ and their interaction on mean space-use requirements and the variance around them. (F) The effect of $\mu(t)$ does not follow the data closely because $E(R)$ and $\text{Var}(R)$ are highly correlated. Consequently, while estimating the effects of $E(R)$ and $\text{Var}(R)$ via separate models would allow result in a closer fit, the estimated effects would be inappropriate because they do not disentangle the effects of $E(R)$ and $\text{Var}(R)$. See Appendix C for additional information. The tapir movement data corresponds to the individual named “Anna” from the Cerrado sample of Medici *et al.* (2022).

296 titative simulations and an empirical case study. Each of the two methods allows us to high-
297 light the strengths and limitations of simulation-based and data-driven approaches, which
298 we discuss below.

299 **Strengths and limitations of the simulation-based approach**

300 The simulations we present here provide a simple and direct estimate of the effects of re-
301 source abundance and stochasticity on organisms' space-use requirements. The combination
302 of simplicity (few drivers of movement) and realism (continuous-time movement models)
303 allowed us to estimate the effects of $E(R)$ and $\text{Var}(R)$ on organisms' space-use requirements
304 using simple causal models of inference without the confounding variables that are often
305 present in empirical data (e.g., predator avoidance, territoriality, competition, landscape
306 connectivity). Additionally, since our sample size was virtually unlimited, we were able to
307 simulate sufficient data to ensure the simulations were stable and the resulting estimated
308 coefficients were well estimated (see Appendix B).

309 Avoiding confounding variables rather than attempting to account for them (as is required
310 with empirical data) allowed us to develop theory easily while providing a baseline model
311 against which one can contrast empirical examples. In figures B6, we present the Directed
312 Acyclical Graph (DAG, see McElreath 2016) we used to infer causal the mechanisms of
313 changes in H and estimate the direct, partial effects of $E(R)$ and $\text{Var}(R)$ on H (contrast
314 this with figure C5 and the section below).

315 By quantifying the deviations from the simple theoretical models, one can then assess the
316 importance of other drivers movement and behavior. Still, the simplicity of the underlying
317 model and its (often invalid) assumptions often limit the applicability of simulated models in
318 realistic scenarios. Responses to $E(R)$ and $\text{Var}(R)$ in real ecosystems likely depend on many
319 other drivers of movement, including competition, movement costs, and predation, which
320 may affect the effects of $E(R)$ and $\text{Var}(R)$ on both $E(H)$ and $\text{Var}(H)$ (Jetz et al. 2004;
321 Noonan et al. 2023). And while it is possible to account for all of these factors through

322 simulations, empirical data often can provide evidence for these effects without the need for
323 complex model structures.

324 **Strengths and limitations of the empirical approach**

325 In the absence of direct measurements of R , empirical models estimating the effects of R on
326 H must depend on proxies of R , such as NDVI. However, using proxies of R rather than
327 direct measurements introduces sources of bias. While R and NDVI are correlated (e.g.,
328 Phillips et al. 2008; Merkle et al. 2016, 2019; Middleton et al. 2018; Geremia et al. 2019;
329 Seigle-Ferrand et al. 2021), the relationship between the two can be weak (Gautam et al.
330 2019) and nonlinear (**ref?**). This is because remote-sensed proxies of R and they do not
331 measure resource availability directly, so they introduce two sources of bias: ecosystem-level
332 biases (indicated as Z in the DAG in figure C5) and satellite-level confounding variables (S
333 in figure C5).

334 Examples of ecosystem-level biases are the effects of competition, predation, habitat
335 connectivity, and movement costs, all of which can depend on habitat quality, and, conse-
336 quently, be correlated nonlinearly to R and *NDVI* (Jetz et al. 2004; Prox and Farine 2020).

337 Resource-rich patches can attract larger amounts of competitors (Kacelnik et al. 1992) and
338 predators, which may increase pressures from competition (**ref?**) and predation (Brown et
339 al. 1999). While such pressures may increase avoidance behaviors, the behaviors may result
340 in both an expansion of the home range (Jetz et al. 2004; Prox and Farine 2020)

341 **here**

342 , but larger home ranges can be harder to defend and also result in higher rates of
343 competition and movement costs (Grant 1993; Jetz et al. 2004; but also see Dickie et al.
344 2022). Additionally, persistent territorial defense from competitors may prevent organisms
345 from using space freely and as necessary (wolves, *Canis lupus*: Rich et al. 2012; feral cats,
346 *Felis catus*: Bengsen et al. 2016; Capuchin monkeys, *Cebus capucinus*: Tórrez-Herrera et
347 al. 2020), so the effect of $E(R)$ on space use may vary between individuals, species, and

348 locations. Still, these pressures simply alter the intensity with which organisms respond to
349 $E(R)$ but not the shape of the relationship, since each of these cases fall along different parts
350 of the continuum in $E(R)$ shown in fig. 1.

351 Due to data limitations, disentangling the effects of such confounds is often complex or
352 impossible (e.g., Wang et al. 2019).

353 Satellite-level confounds include coarse spatiotemporal resolution (and the consequent
354 aggregation of signals, see ref?), satellite-level error (Tian et al. 2015; Fan and Liu 2016;
355 Huang et al. 2021), and other limitations of remote sensing, including the inability to quan-
356 tify the abundance of specific resources, whether these be preferred forage or the distribution
357 of prey. In the case of preferences for intermediate values of NDVI [e.g., young grass rather
358 than mature grasslands, see @], nonlinear models such as Generalized Additive Models can
359 help account for a nonmonotonic relationship between H and $E(NDVI)$, as long as data
360 are sufficiently abundant to avoid any artifacts due to data paucity. In the case study we
361 present here, sampling limitations resulted in a strong nonlinear correlation between $E(R)$
362 and $\text{Var}(R)$, which prevented us from estimating any nonlinear preferences in mean NDVI
363 (i.e., the proxy for $E(R)$). A tracking time series of two or more years or additional individ-
364 uals would have provided better estimates, but that was beyond the scope of this paper.

365 Modeling the tapir's space use as a function of resource abundance alone would result in
366 an excessively strong estimated effect and a quantifiably worse model fit ($\Delta\text{AIC} \approx 87$, see
367 Appendix C). By including the effect of $\sigma^2(t)$ in the model along with that of $\mu(t)$, we show
368 that the tapir responds to both resource abundance and stochasticity. While the tracking
369 period may be too short to see the effects of $E(R)$ clearly, it should also be noted that the
370 Cerrado is relatively rich in vegetation throughout the entire year (fig. 6A), and thus the tapir
371 does not experience resource scarcity during the tracking period. Consequently, this example
372 demonstrates two points central to this paper. Firstly, even animals in resource-rich regions
373 such as the Brazilian Cerrado adapt their behavior in response to reosurce stochasticity.
374 Secondly, trends in mean resources alone are not sufficient to explain the tapir's space use,

³⁷⁵ and the stochasticity in R is an important driver of the tapir's movement.

³⁷⁶ **Adaptations to changes in $E(R)$ and $\text{Var}(R)$**

³⁷⁷ Paragraphs to tie in:

- Rizzuto et al. (2021) found that the space-use requirements of snowshoe hares (*Lepus americanus*) increased with average carbon to nitrogen ratio (C:N, a measure of N scarcity) in lowbush blueberry as well as the coefficient of variation (the standard deviation divided by the mean, $\frac{\sqrt{\sigma^2(t)}}{\mu(t)}$) in C:N. However, it is hard to determine how $\sigma^2(t)$ affected the hares' space-use requirements since the coefficient of variation is a function of both $\mu(t)$ and $\sigma^2(t)$, so the effects of the two variables are confounded. Similarly, Mueller et al. (2011) suggested that ecosystem variability (measured as spatial semivariance in NDVI) causes ungulates to move more and adopt more nomadic behaviors, but it is hard to determine whether the higher semivariances in NDVI are due to an increase in $\text{Var}(R)$ or simply spatial changes in $E(R)$ (e.g., increased seasonality or continentality). Likewise, Herfindal et al. (2005) found that the home ranges of Canadian lynx (*Lynx canadensis*) decreased with seasonality, but this may be an artifact of a lower $\mu(t)$ in highly seasonal environments, rather than stochasticity in R . A subsequent analysis by Nilsen et al. (2005) of 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 seasonality, which suggests that different species may have different perceptions of the changes in R over the seasons. Collectively, these studies provide support towards the effects of both $E(R)$ and $\text{Var}(R)$ on organisms' space-use requirements, but the lack of a unifying framework across these studies makes it challenging to synthesize their findings. Thus, it is important to disentangle the effects of changes in $E(R)$, such as seasonal trends in $\mu(t)$, and stochasticity ($\text{Var}(R)$). The need to account for changes in both $E(R)$ and $\text{Var}(R)$ is compounded by recent changes in climate, which expose species to

401 novel situations and increasingly common and extreme stochastic events (Noonan et
402 al. 2018; Yao et al. 2022; Intergovernmental Panel On Climate Change 2023).

- 403 • Nilsen et al. (2005) also show that the effect of $E(R)$ on the home-range size of wolves
404 and fishers (*Martes pennanti*) depends on seasonality (and vice-versa), since organisms
405 in habitats with high and low seasonality had opposite responses to $E(R)$. Therefore,
406 it may not be sufficient to account for the effects of $E(R)$ and $\text{Var}(R)$; models may also
407 need a term for interaction between the two. This may be because organisms respond
408 strongly to $\sigma^2(t)$ when $\mu(t)$ is low, but they may not respond if $\mu(t)$ is sufficiently high.
409 However, it does not explain why organisms may respond to $E(R)$ in opposite ways in
410 different habitats. Instead, we suspect this inconsistency is because Nilsen et al. (2005)
411 do not distinguish between changes in $\mu(t)$ and $\sigma^2(t)$ between seasons, so the effects
412 of the two are confounded in the seasonality term. Distinguishing between changes in
413 $E(R)$ and $\text{Var}(R)$ allows one to separate the two seasonal cycles and produce more
414 consistent results.

415 The spatiotemporal scale over which an event occurs is a main determinant of whether an
416 organism will be able to predict the event and how it will respond to it (or fail to do so).

417 Events that occur at the scale of the organism (i.e. approximately one or more times per
418 generation and on the spatial scale of the organism's spatial range, see Frankham and Brook
419 2004) are more likely to be perceived as a threat or boon worth preparing for (Foley et
420 al. 2008; Berger et al. 2018; Geremia et al. 2019). Consequently, organisms with long
421 generations (e.g., elephants, *Loxodonta sp.*) or large spatial ranges (e.g., migratory birds)
422 are more likely to experience stochastic events and thus are also more likely to respond to and
423 prepare for them. Animals may adapt by adjusting the timing of reproduction (Southwood
424 1977; Boersma et al. 2021) and torpor or hibernation (Inouye et al. 2000; Goldberg and
425 Conway 2021), or storing large amounts of energy (Lindstedt and Boyce 1985) through fat
426 storage (Armitage et al. 2003; Nespolo et al. 2022) or resource caching (Post et al. 2006).

427 Alternatively, animals may alter their movement and travel long distances over short periods

428 of time (Jetz et al. 2004; Hirt et al. 2017), whether this be for migration (Mueller et al.
429 2013; Geremia et al. 2019) or nomadism (Teitelbaum et al. 2015; Nandintsetseg et al. 2019;
430 Teitelbaum and Mueller 2019). Over the years, animals may also develop more complex
431 cognitive abilities (Brown et al. 2004), including the development of memory (Foley et al.
432 2008; Fagan et al. 2013; Polansky et al. 2015; Abrahms et al. 2019; Geremia et al. 2019;
433 Rickbeil et al. 2019; Riotte-Lambert and Matthiopoulos 2020; Steixner-Kumar and Gläscher
434 2020; Falcón-Cortés et al. 2021; Cavedon et al. 2022; Ranc et al. 2022), which is required
435 for migration (Mueller et al. 2013; Middleton et al. 2018; Abrahms et al. 2019; Geremia
436 et al. 2019; Merkle et al. 2019; Rickbeil et al. 2019; but see: Cuadrado 2021; Stefanescu
437 et al. 2021). However, adapting to changes in environmental cues rather than relying on
438 memory alone (Jonzén et al. 2006; Büntgen et al. 2017; Rickbeil et al. 2019; Severson et al.
439 2021), can prevent animals from becoming trapped in sub-optimal conditions (Abrahms et
440 al. 2019).

441 In contrast, individuals with short lifespans are less likely to experience stochastic events
442 and develop memory about them. However, the short generation time and high reproductive
443 rate of r-selected species (as opposed to k-selected species, see Pianka 1970; Brown et al.
444 2004) may promote other traits that increase survival following extreme events. Examples in-
445 clude higher population size, dispersal, higher genetic diversity, and complex group dynamics
446 (e.g., Cuadrado 2021; Stefanescu et al. 2021). Events that occur over large spatiotemporal
447 scales can thus promote slow, large-scale changes through the adaptation, natural selection,
448 and evolution of the species (Gienapp et al. 2008; Logares and Nuñez 2012; Anderson et
449 al. 2017; Grant et al. 2017), which is more likely to adapt if starting populations are large
450 with high genetic diversity and short generations, as in the case of r-selected species (but see
451 Leung 2022). Of course, an organism with a lifespan shorter than a year will be unable to
452 experience the cyclical nature of the seasons, and an organism with a lifespan of a few weeks
453 or days may not even experience substantial changes in weather other than daily cycles and
454 some weather stochasticity. Still, a population may respond to spatiotemporal cycles in

455 $E(R)$ and $\text{Var}(R)$ by adapting the group's reproduction timing and migration (e.g., painted
456 lady butterflies: Cuadrado 2021; Stefanescu et al. 2021).

457 A population's fitness and chances of survival in a changing environment depend strongly
458 on its adaptability and responsiveness to change (Riotte-Lambert and Matthiopoulos 2020),
459 and its ability to recognize cues that precede extreme events or periods of scarcity or abun-
460 dance can have appreciable effects on its members' chances of survival and reproduction.
461 For example, ungulates' ability to time their yearly migrations on available forage biomass,
462 snow fall, snow melt, and hunting pressure allow them to adapt to changes in both $E(R)$ and
463 $\text{Var}(R)$, while their spatial memory (Falcón-Cortés et al. 2021; Ranc et al. 2022) allows them
464 to optimize their large-scale movement by reducing the amount of time and energy spent
465 exploring. Similarly, the ability of trans-Saharan migrant birds to adapt their migration
466 timing based on environmental cues allows them to account for differences in $\mu(t)$ between
467 years (Jonzén et al. 2006). However, relying too strongly on short-term changes rather than
468 depending on long-term memory can also cause animals to fail to find crucial resources dur-
469 ing unpredictable times (whooping cranes: Mueller et al. 2013; Foley et al. 2008; elephants:
470 Polansky et al. 2015; whales: Abrahms et al. 2019). Instead, if anomalies occur repeatedly
471 over time, organisms may adapt to a higher $\sigma^2(t)$ or shift their ranges altogether (terrestrial
472 animals: Chen et al. 2011; Büntgen et al. 2017; ungulates: Severson et al. 2021), including
473 migratory animals (Jonzén et al. 2006). Still, while range shifts can help species overcome
474 changes in the long-term trends in $\mu(t)$ and $\sigma^2(t)$, including changes in phenology (Severson
475 et al. 2021), they can also result in phenological mismatches (Lameris et al. 2018) and add
476 pressure to the species that already live in the habitat (e.g., Wallingford et al. 2020; but see
477 Shepard et al. 2022), including specialists and obligate symbionts that may be unable to
478 shift their range, since it is determined by their food sources' and associates' ability to move
479 and adapt, too.

⁴⁸⁰ **Conclusion**

⁴⁸¹ The work presented here provides a unifying framework for viewing movement as a function
⁴⁸² of resource abundance and stochasticity. We provide realistic and flexible hypotheses of
⁴⁸³ the effects of $E(R)$ and $\text{Var}(R)$ on organisms' space-use requirements and movement behav-
⁴⁸⁴ ior. We demonstrate that organisms' space-use requirements respond nonlinearly to both
⁴⁸⁵ resource abundance and stochasticity, and we demonstrate the importance of accounting
⁴⁸⁶ for $\text{Var}(R)$ besides $E(R)$. We also provide a moving window approach that allows one to
⁴⁸⁷ model movement continuously rather than imposing arbitrary thresholds between different
⁴⁸⁸ periods or types of behaviors, including temporal changes in space-use requirements and
⁴⁸⁹ shifts between range-residency and nomadism. The methods presented here can be applied
⁴⁹⁰ to assess the current and future quality of protected areas while also estimating the amount
⁴⁹¹ of space organisms currently need and will need in the future under different climate change
⁴⁹² scenarios.

⁴⁹³ **Conflict of interest**

⁴⁹⁴ The authors declare there are no conflicts of interest.

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