

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

Article type: Major article

Words in abstract: 199

Words in main text: 5579

Figures: 6

Tables: 0

References: 102 (updated on 2024-04-12)

Appendices: 3

Key words: energetics, energetic landscape, environmental stochasticity, space use, spatial needs, ctmm

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, unlike other***
43 ***areas of ecological research, findings from these studies are not structured***
44 ***around a set of theoretical expectations.*** Instead, results are typically reported as
45 independent, novel findings. Thus, there remains a need for a clear hypothesis for the effects
46 of resource abundance on organisms' space-use requirements. Additionally, while much work
47 has been done on estimating organisms' responses to average resource abundance, there
48 is little information on how they respond to unpredictable changes in resources (but see:
49 Stephens and Charnov 1982; Rizzuto et al. 2021).

50 Here, we refer to a location's average amount of resources as "resource abundance",
51 while we use the phrase "resource stochasticity" to indicate the variability in resources after
52 accounting for changes in the mean. We argue that, on its own, a habitat's long-term
53 resource abundance is not sufficient to assess the habitat's quality, nor make predictions
54 about how much space an organism might use. For instance, herbivores in a grassland with
55 relatively low but constant forage availability (low mean and variance) will adopt different
56 behaviors and adaptations from herbivores in a desert with equally scarce forage but rare,
57 sudden, and strong pulses of resources (low mean and high stochasticity). In the grassland,
58 an animal may require a large but constant home range as it moves between patches in
59 search of food (Teitelbaum and Mueller 2019), while an animal in the desert may switch
60 between dispersal in search for high-resource patches and short-term range residency ***within***
61 patches (Charnov 1976). Although the two habitats may have the same long-term average
62 resource abundance, the ephemerality of resource in the second environment would promote
63 a different selection of movement and life history strategies. Overall, resource stochasticity
64 may decrease organisms' fitness and landscapes' energetic balances (Chevin et al. 2010), but
65 there is still limited empirical evidence to support this hypothesis (but see: Herfindal et al.
66 2005; Nilsen et al. 2005; Rizzuto et al. 2021).

67 Here, we illustrate how organisms' space use ***should be expected to*** depend on both

the abundance and unpredictability of resources. First, we set the theoretical background necessary for the successive sections by introducing key concepts and notation. Next, we provide a review of the effects of resource abundance on organisms' space use while suggesting a unifying hypothesis. Afterwards, we provide a review of the effects of resource stochasticity on organisms' space use while suggesting a second unifying hypothesis. Subsequently, we demonstrate the power of these two hypotheses using quantitative, simulated 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 (*Tapirus terrestris*) from the Brazilian Cerrado (Medici et al. 2022). 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.

Resources as a random variable

Resources are often unpredictable (and difficult to quantify), since they depend on various factors which cannot be accounted for easily, including climate (Lindstedt and Boyce 1985; Morellet et al. 2013; Schmidt et al. 2020), weather (Morellet et al. 2013; Fjelldal et al. 2021), competitive pressure (Rich et al. 2012; Tórrez-Herrera et al. 2020), and differences in energetics at the individual (Schmidt et al. 2020) and species level (Jetz et al. 2004). **Thus**, ***we can treat the amount of resources at a given point in space (u) and time (t) as a random variable, denoted $R(u,t)$. The benefit of treating resources as a numerical random variable, is that it*** provides us with the capacity to leverage techniques from probability theory and statistics. We assume readers are familiar with fundamental statistical concepts (e.g., random variables, probability distributions, expected value and variance of a random variable), but we define and explain the necessary concepts in Appendix A.

92 **Effects of resource abundance, $E(R)$**

93 While organisms' needs vary greatly between taxonomic groups, some needs are essential
94 for most species for survival and reproduction. All heterotrophic organisms require sources
95 of chemical energy (i.e., food), water, and various limiting nutrients to survive, grow, and
96 reproduce (Harvey and Clutton-Brock 1981; Baldwin and Bywater 1984; Reich 2001). **As**
97 *the abundance of essential resources fluctuates*, motile organisms can move to new
98 locations *or 'patches'*, *to meet their requirements* (Charnov 1976; Brown et al. 1999),
99 but they must also account for a higher metabolism and movement costs (Taylor et al. 1982).

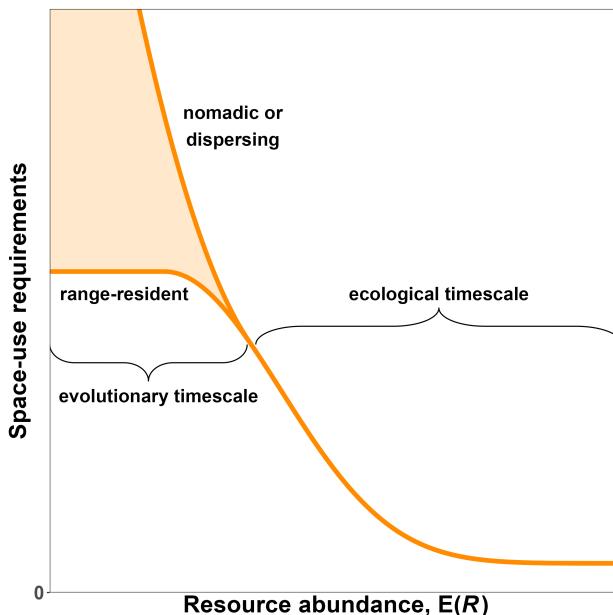


Figure 1: Hypothesized space-use requirements of an organism as a function of resource abundance ($E(R)$). We expect low values of $E(R)$ to result in high space-use requirements as organisms are forced to explore large areas to collect the resources they require to survive, whether they be range-resident 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 $E(R)$.

100 Fig. 1 illustrates our first of two hypotheses: When $E(R)$ is high, we expect organisms'
101 spatial requirements to be relatively small and near the smallest amount of space required
102 to survive (e.g., Relyea et al. 2000; Herfindal et al. 2005; Nilsen et al. 2005). At lower
103 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 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). ***moved from above*** 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, ***conceptually***, the relationship between space-use requirements and $E(R)$ must be nonlinear, since: (1) there ***is an upper limit*** to how much space an organism is able to explore in its lifetime and (2) the minimum amount of space it requires to survive ***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).

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.

¹³¹ However, if $\mu(t)$ changes repetitively and regularly over time (e.g. peaks each spring and is
¹³² lowest in winter), an organism may learn to predict times of high or low $E(R)$ (Samarra et
¹³³ al. 2017; Abrahms et al. 2019; Geremia et al. 2019; e.g., Falcón-Cortés et al. 2021) but will
¹³⁴ still not be able to predict R exactly.

¹³⁵ **Effects of resource stochasticity, $\text{Var}(R)$**

¹³⁶ The example illustrated in the section above can occasionally be a useful simplification of
¹³⁷ relatively stable environments or when ***information on how $E(R)$ changes is limited***,
¹³⁸ but it likely not realistic, since ***the variance in R around $E(R)$, which we indicate***
¹³⁹ ***as $\text{Var}(R)$, can also differ between locations or time periods***. Generally, periods
¹⁴⁰ of scarcity (e.g., winter, droughts) not only have lower $E(R)$ but also have narrower ranges
¹⁴¹ of R , ***which implies a smaller $\text{Var}(R)$*** . In contrast, periods of high $E(R)$ (e.g., spring
¹⁴² green-up) also often tend to have higher $\text{Var}(R)$, ***as R tends to vary more (e.g., due***
¹⁴³ ***differences in phenology, environmental conditions, and patch depletion by***
¹⁴⁴ ***competitors). Recognizing differences in $\text{Var}(R)$ between locations or periods***
¹⁴⁵ ***helps account for the small-scale stochasticity in R , after accounting for the***
¹⁴⁶ ***large-scale average R (Levin 1992)***. ***However***, when both $E(R)$ and $\text{Var}(R)$ change
¹⁴⁷ over time (fig. A2), predicting R becomes more complex, since disentangling changes in $E(R)$
¹⁴⁸ and $\text{Var}(R)$ is not simple (Steixner-Kumar and Gläscher 2020). Statistically, this is because
¹⁴⁹ the more change one attributes to $\mu(t)$ (i.e., the wigglier it is), the smaller $\sigma^2(t)$ becomes.
¹⁵⁰ Conversely, the smoother $\mu(t)$ is, the larger $\sigma^2(t)$ becomes. Biologically, this is important
¹⁵¹ because an organism's perception scale (Levin 1992) determines whether it sees a change in
¹⁵² R as a trend in $E(R)$ or as a stochastic event (i.e., due to $\text{Var}(R)$). An organism's perception
¹⁵³ of changes in R will also depend strongly on its cognitive capacities and memory (Foley
¹⁵⁴ et al. 2008; Fagan et al. 2013; Mueller et al. 2013; Abrahms et al. 2019; Falcón-Cortés et
¹⁵⁵ al. 2021). Whether, an organism is able to predict trends in $\sigma^2(t)$ or not, environmental
¹⁵⁶ variability is thought to reduce a landscape's energetic balance (Chevin et al. 2010), which,

157 in turn, decreases organisms' fitness (e.g., Berger et al. 2018) and increases their space-use
158 requirements. While this is true for both predictable and unpredictable stochasticity, extreme
159 and rare events are more likely to have a stronger effect due to their unpredictability and
160 magnitude (Logares and Nuñez 2012; Anderson et al. 2017). A few recent studies support
161 these hypotheses (Chevin et al. 2010; Morellet et al. 2013; Nandintsetseg et al. 2019;
162 Riotte-Lambert and Matthiopoulos 2020), but many of them are limited in geographic and
163 taxonomic scales, so the extent to which these preliminary findings can be generalized is
164 ***unknown***. Thus, there remains a need for developing a more complete understanding of
165 how organisms' space-use requirements change with environmental stochasticity.

166 Similarly to $E(R)$, we hypothesize $\text{Var}(R)$ to have a nonlinear effect on organisms' space-
167 use requirements. When $\text{Var}(R)$ is low enough that R is relatively predictable, we do not
168 expect changes in $\text{Var}(R)$ to have a noticeable effect. But as resources become increasingly
169 unpredictable, we expect space-use requirements to increase progressively faster (fig. 2) be-
170 cause: (1) as $\text{Var}(R)$ increases, the chances of finding low R increase superlinearly, (2)
171 stochastic environments tend to be less productive (Chevin et al. 2010), (3) stochasticity
172 reduces an organism's ability to specialize and reduce competition for R (Levins 1974), and
173 (4) the added movement required to search for food increases organisms' energetic require-
174 ments. If resources remain highly unpredictable over long periods of time (e.g., multiple
175 lifespans), organisms may evolve or develop new behaviors (such as nomadism, dispersal,
176 and migration) or adaptations (such as increased fat storage or food caching). If changes in
177 $\sigma^2(t)$ are sufficiently predictable, organisms may learn to anticipate and prepare for periods
178 of greater stochasticity by pre-emptively caching food, migrating, or relying on alternative
179 food sources during stochastic events (e.g., the seasonal arrival of competitors).

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

181 We have provided the case for why both $E(R)$ and $\text{Var}(R)$ ***should be expected to*** affect
182 organisms' space-use requirements, but we presented the two parameters as independent

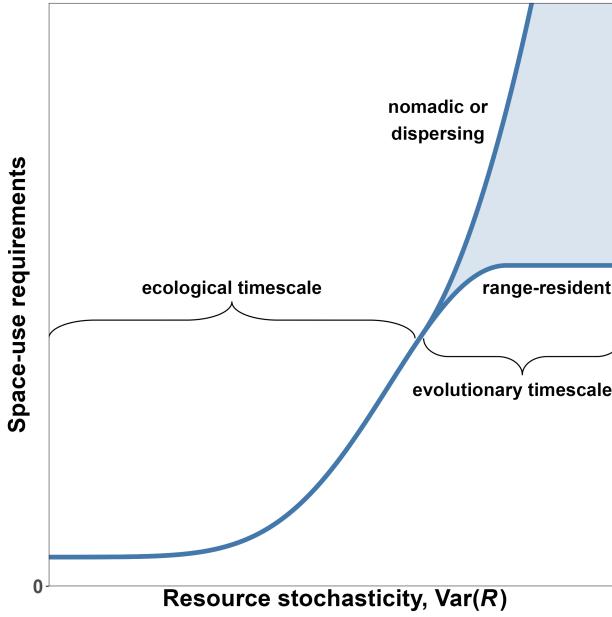


Figure 2: Hypothesized space-use requirements of an organism as a function of resource stochasticity ($\text{Var}(R)$). We expect low values of $\text{Var}(R)$ to result in low space-use requirements as organisms are able to depend on relatively predictable resources. As $\text{Var}(R)$ increases, space-use 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 $\text{Var}(R)$.

183 drivers of movement. However, organisms may respond to changes in $\text{Var}(R)$ more when
 184 resources are scarce than when they are abundant. Consequently, ***an organism's move-***
 185 ***ment behavior is likely to be a function of*** not only the marginal effects of $E(R)$
 186 and $\text{Var}(R)$ but also their interactive effects. A highly unpredictable habitat may be very
 187 inhospitable if resources are poor, but $\text{Var}(R)$ may have little effect if resources are stochas-
 188 tic but always abundant. Thus, we expect $\text{Var}(R)$ to have a stronger effect on space-use
 189 requirements when $E(R)$ is low, and less of an effect when $E(R)$ is high. We explore this
 190 more in the following section.

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

192 To support our hypotheses of how organisms' space use is affected by $E(R)$, $\text{Var}(R)$, and the
 193 interaction effect of $E(R)$ and $\text{Var}(R)$, we present the results from a series of quantitative
 194 simulations. To start, we used the `ctmm` package (Fleming and Calabrese 2021) for `R` (`R`

195 Core Team 2023) to generate 200 tracks (see Appendix B for sensitivity analyses) from
196 an Integrated Ornstein-Uhlenbeck movement model (IOU model, see Gurarie et al. 2017).
197 The IOU model's correlated velocity produces realistic tracks with directional persistence,
198 but, unlike Ornstein-Uhlenbeck (OU) and Ornstein-Uhlenbeck Foraging (OUF) models, IOU
199 models do not produce spatially stationary movement, so the organism is not range-
200 resident. Consequently, each track is spatially unrestricted and can be interpreted as purely
201 exploratory movement.

202 Each of the 200 tracks were placed on a raster (*this was a raster. is “grid” more*
203 **understandable?**) with common starting point $\langle 0, 0 \rangle$ and sufficient time between tracks to
204 be independent of one another (other than the starting point). Each time the track moved
205 to a new cell, the organism collected resources R sampled from a Gamma distribution. The
206 mean and variance of the distribution were defined by deterministic functions $\mu(t)$ and $\sigma^2(t)$
207 (orange and blue lines in fig. 3). The value of t was constant within each set of 200 tracks, so
208 the time spent moving by the organism in each track did not affect the distribution R was
209 sampled from. Tracks were truncated once the organism reached satiety, and the organism
210 was given enough time to return to $\langle 0, 0 \rangle$ independently from the following track. Finally,
211 as each set of 200 truncated was now spatially restricted and centered around $\langle 0, 0 \rangle$, the
212 set of tracks was modeled to calculate the 95% utilization distribution from an OUF model
213 and Autocorrelated Kernel Density Estimate. We designed the simulations presented here
214 to estimate the effects of $E(R)$ and $\text{Var}(R)$ in simplistic environments. Consequently, we
215 made the following **five** assumptions: (1) $E(R)$ and $\text{Var}(R)$ are constant over space and
216 short periods of time (i.e., within each set of 200 tracks, but not over t). (2) Organisms
217 move randomly in the environment with no energetic costs. (3) Organisms have no percep-
218 tive range or memory, so they are unable to detect, learn, or predict where resources are
219 abundant (high $E(R)$) or reliable (low $\text{Var}(R)$) over time. (4) Resources do not deplete,
220 and there is no competition or predator avoidance. (5) *Since $\mu(t)$ and $\sigma^2(t)$ are spa-*
*221 **tially homogeneous for a given t , organisms respond to $E(R)$ and $\text{Var}(R)$ by***

adapting the extent of the spatial needs (i.e., their positional variance), rather than dispersing or abandoning a range (i.e., their mean location). Additional information is provided in Appendix B, including the directed acyclical graph (see figure B6 and McElreath 2016) we used to infer causal the mechanisms of changes in H and estimate the direct, partial effects of $E(R)$ and $\text{Var}(R)$ on H (contrast this with figure C5 and the empirical case study below).

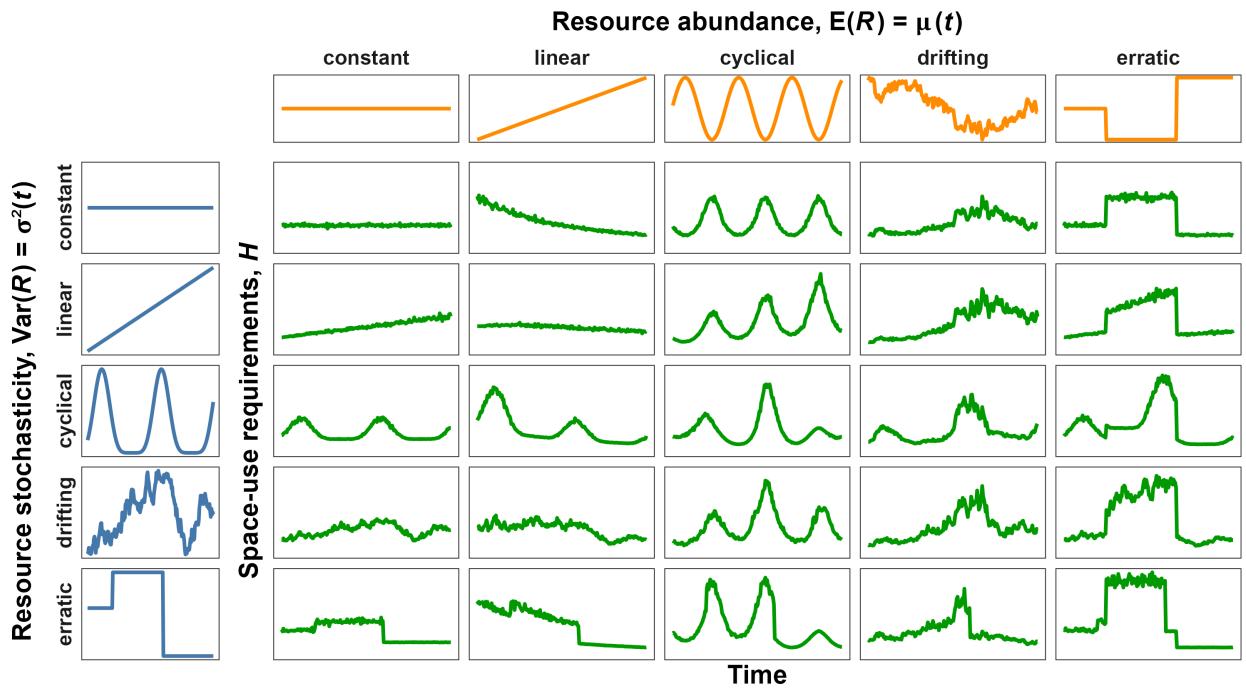


Figure 3: Simulated home range sizes, H , of an organism living in habitats where the mean and variance in resources are constant, linearly increasing, cyclical, drifting, or erratic over time (and homogenous over space). Note how H decreases nonlinearly as $\mu(t)$ increases and increases nonlinearly 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.

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

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

243 The remaining panels in fig. 3 illustrate $E(R)$ and $\text{Var}(R)$ jointly affect H and how
244 complex the effects can be. Since $E(R)$ and $\text{Var}(R)$ have opposite effects on H , disentangling
245 the effects can be particularly difficult when both parameters change in a correlated manner
246 (e.g., linear $E(R)$ and $\text{Var}(R)$). When both $E(R)$ and $\text{Var}(R)$ increase linearly, H initially
247 increases since the effect of $\text{Var}(R)$ is stronger, but then decreases as the effect of $E(R)$ begins
248 to dominate. Difficulties in disentangling the two effects are explored in greater depth in the
249 case study in the following section.

250 ***changed the paragraph below***

251 Although the temporal trends in fig. 3 are complex and the effects of $E(R)$ and $\text{Var}(R)$ can
252 be hard to disentangle, two ***surprisingly (I don't think they're surprising, especially***
253 ***after our rationale)*** simple relationships emerge when H is shown as a function of either
254 $E(R)$ or $\text{Var}(R)$, rather than time (panels A and B of fig. 4A-C). The estimated relationships
255 follow the hypotheses we presented in figs. 1 and 2, although we found that the effect of
256 $\text{Var}(R)$ at average $E(R)$ was linear with a slight sublinear saturation as $\text{Var}(R)$ increased.
257 However, notice that the effect of $\text{Var}(R)$ on $E(H)$ depends strongly on $E(R)$ (panel C).
258 The increase in $E(H)$ over $\text{Var}(R)$ is strongly nonlinear at low values of $E(R)$, but it is not
259 affected by $\text{Var}(R)$ much when $E(R)$ is very low (and $E(H)$ is consequently very high). As
260 expected by the changes in the spread of the points in panels A and B of figure 4, the variance
261 in H also depends on $E(R)$ and $\text{Var}(R)$ (figure 4D-F). Since we modeled H using a Gamma

family of distributions, we expected $\text{Var}(H)$ to increase with $E(H)$, but the location-scale model removes the assumption of a constant mean-variance relationship. Flexibility in the mean-variance relationship to change over $E(R)$ and $\text{Var}(R)$, allowed us to show the strong exponential effect of $E(R)$ and $\text{Var}(R)$ on $\text{Var}(H)$. Consequences of these effects are explored in the discussion section.

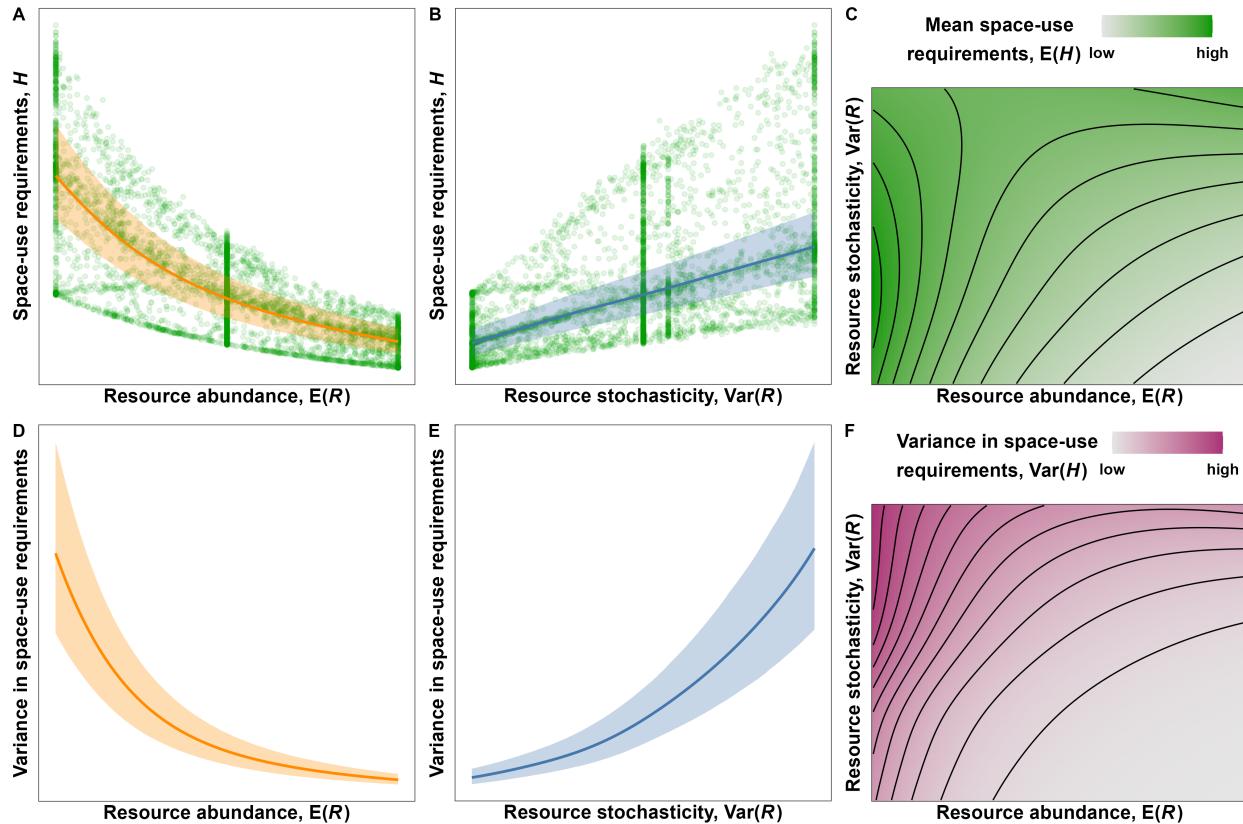


Figure 4: Effects of $E(R)$ and $\text{Var}(R)$ on simulated spatial requirements with 95% Bayesian credible intervals for the mean. While the effect of $\text{Var}(R)$ is sublinear in panel B, the effect of $\text{Var}(R)$ depends strongly on $E(R)$ (see panel C). Credible intervals were calculated 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.

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

The simulations in the section above mostly follow the hypotheses we presented in the introduction, but they are based on assumptions that are often not met in real natural environments. Organisms live in spatiotemporally heterogeneous and dynamic environments,

which the development of perceptual ranges, navigation, and memory. Together, these abilities result in selective space use that depends on resource availability (Kacelnik et al. 1992) and resource depletion (Charnov 1976).

In this section, we test the hypotheses illustrated in the introduction using empirical tracking data on a lowland tapir from the Brazilian Cerrado along with estimates of $E(R)$ and $\text{Var}(R)$ using the Normalized Difference Vegetation Index (NDVI, see Pettorelli et al. 2011), a remote-sensed measure of landscape greenness, as a proxy of forage abundance. Appendix C contains additional information on how NDVI was modeled along with details on the continuous-time movement models (Noonan et al. 2019a; Fleming and Calabrese 2021) and autocorrelated kernel density estimation (Noonan et al. 2019b; Alston et al. 2022; Silva et al. 2022) used to quantify the tapir’s space-use requirements. Through this example, we aim to provide support for the two hypotheses using empirical data that do not depend on as 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. 5 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 (GAMLS, theory: Rigby and Stasinopoulos 2005; Stasinopoulos and Rigby 2007; examples: Bjorndahl et al. 2022; Mariën et al. 2022; Gushulak et al. 2024) 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 low number of knots ($k = 3$). Additional information is provided in appendix C. Overall, the results presented in fig. 5 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.

307 Discussion

This paper presents two hypotheses *that describe* the effects of resource abundance and stochasticity on organisms' space-use requirements. *We show that, together, these hypotheses provide a framework for understanding how organisms adapt their spatial needs to both average conditions and the variance around the average conditions. By moving beyond considering only average conditions, we are able to create a more realistic view of how animals respond to changes in both predictable and unpredictable environmental conditions. We support the hypotheses using quantitative simulations and test it using a simple case study with methods that can implemented easily by animal movement ecologists (see Appendix C). In this section, we discuss the strengths and limitations of both the simulation-based and empirically driven approaches along with comments on the consequences for free-moving animals in a changing world.*

320 Strengths and limitations of the simulation-based approach

The simulations we present here provide a simple and direct estimate of the effects of resource abundance and stochasticity on organisms' space-use requirements. The combination

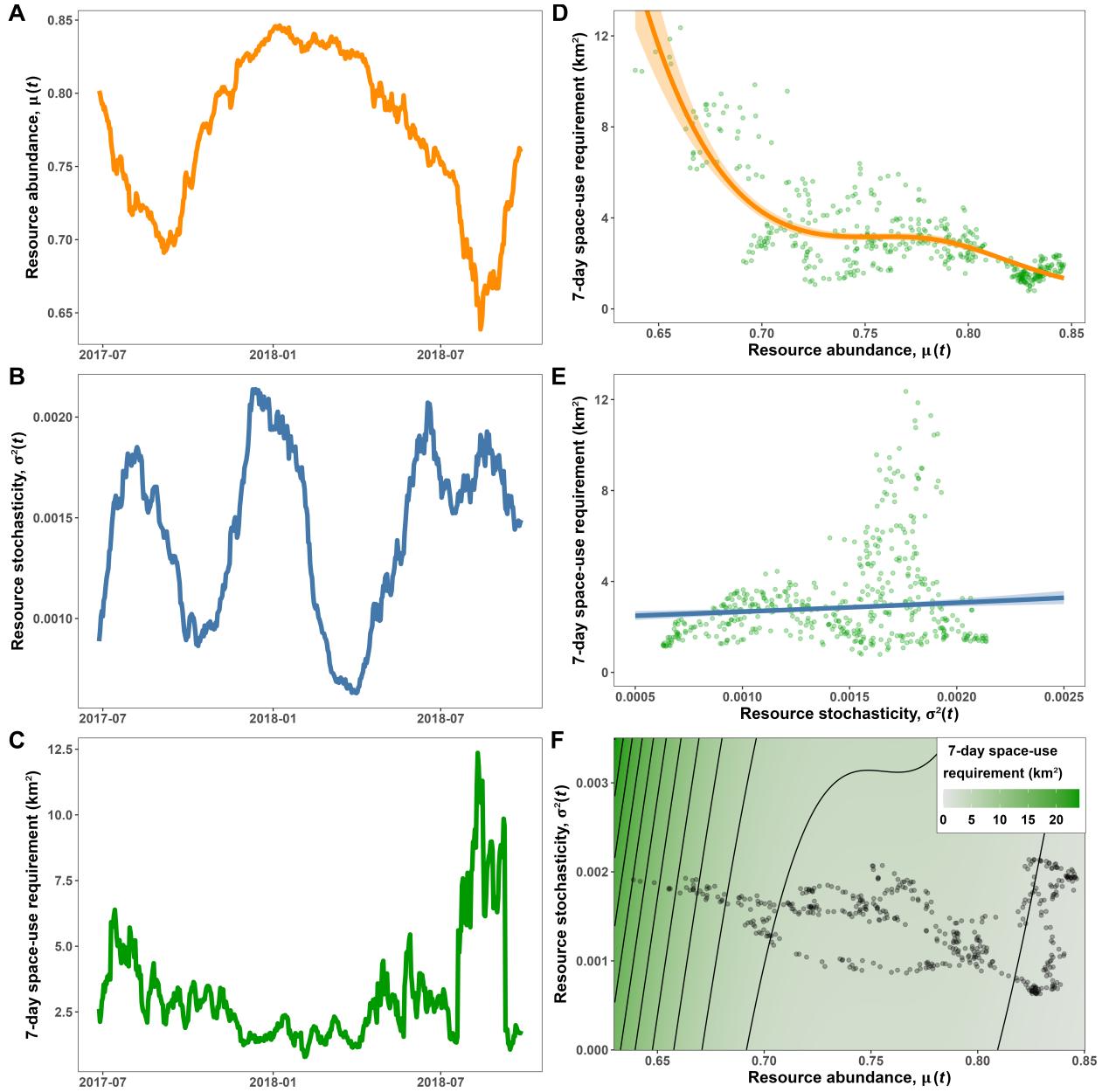


Figure 5: Seven-day home-range size of a lowland tapir (*Tapirus terrestris*) in response to changes in mean and variance in resources. (A) Trends in resource abundance over time, $\mu(t)$, estimated as the average mean NDVI at the locations visited by the tapir during a seven-day period. (B) Variance 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).

323 of simplicity (few drivers of movement) and realism (continuous-time movement models)
324 allowed us to estimate the effects of $E(R)$ and $\text{Var}(R)$ on organisms' space-use requirements
325 using simple causal models of inference without the confounding variables that are often
326 present in empirical data (e.g., predator avoidance, territoriality, competition, landscape
327 connectivity). Additionally, since our sample size was virtually unlimited, we were able to
328 simulate sufficient data to ensure the simulations were stable and the resulting estimated
329 coefficients were well estimated (see Appendix B).

330 Avoiding confounding variables rather than attempting to account for them (as is *often*
331 required with empirical data) allowed us to develop theory easily while providing a baseline
332 model against which one can contrast empirical examples.

333 By quantifying the deviations from the simple theoretical models, one can then assess the
334 importance of other drivers movement and behavior. Still, the simplicity of the underlying
335 model and its (often invalid) assumptions often limit the applicability of simulated models in
336 realistic scenarios. Responses to $E(R)$ and $\text{Var}(R)$ in real ecosystems likely depend on many
337 other drivers of movement, including competition, movement costs, and predation, which
338 may affect the effects of $E(R)$ and $\text{Var}(R)$ on both $E(H)$ and $\text{Var}(H)$ (Jetz et al. 2004;
339 Noonan et al. 2023). And while it is possible to account for all of these factors through
340 simulations, empirical data often can provide evidence for these effects without the need for
341 complex model structures.

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

343 In the absence of direct measurements of R , empirical models estimating the effects of R on
344 H must depend on proxies of R , such as NDVI. However, using proxies of R rather than
345 direct measurements introduces sources of bias. While R and NDVI are correlated (e.g.,
346 Phillips et al. 2008; Merkle et al. 2016, 2019; Middleton et al. 2018; Geremia et al. 2019;
347 Seigle-Ferrand et al. 2021), the relationship between the two can be weak (Gautam et al.
348 2019), satellite-dependent, and nonlinear (Fan and Liu 2016; Huang et al. 2021). This is

349 because remote-sensed proxies of R and they do not measure resource availability directly,
350 so they introduce two sources of bias: ecosystem-level biases (indicated as Z in the directed
351 acyclical graph in figure C5) and satellite-level confounding variables (S in figure C5).

352 Examples of ecosystem-level biases are the effects of competition, predation, habitat
353 connectivity, and movement costs, all of which can depend on habitat quality, and, conse-
354 quently, be correlated nonlinearly to R and NDVI (Jetz et al. 2004; Prox and Farine 2020).
355 Resource-rich patches can attract larger amounts of competitors (Kacelnik et al. 1992) and
356 predators, which may increase pressures from competition and predation (Charnov 1976;
357 Brown et al. 1999). While such pressures may increase avoidance behaviors, avoidance may
358 have a complex effect on H , since it can result in both an expansion of the home range (Jetz
359 et al. 2004; Prox and Farine 2020) or a contraction of an animal's movement, since larger
360 home ranges can be harder to defend and also result in higher movement costs (Grant 1993;
361 Jetz et al. 2004). Additionally, persistent territorial defense from competitors may prevent
362 organisms from using space freely and as necessary ***under the Ideal Free Distribution***
363 (theoretical framework: Fretwell and Lucas 1969; examples: Rich et al. 2012; Bengsen et al.
364 2016; Tórrez-Herrera et al. 2020).

365 Satellite-level confounds include information loss due to coarse spatiotemporal resolution
366 (Fan and Liu 2016; Huang et al. 2021), satellite-level error (Tian et al. 2015; Fan and
367 Liu 2016; Huang et al. 2021, 2021), and other limitations of remote sensing (e.g., inability
368 to quantify specific resources, competitive pressure, and predator avoidance). However,
369 nonlinear models such as Generalized Additive Models (Wood 2017) can help account for
370 preferences for intermediate values of NDVI (e.g., young grass rather than mature grasslands,
371 see Huang et al. 2021). In the case study we present here, sampling limitations resulted in
372 a strong nonlinear correlation between $E(R)$ and $\text{Var}(R)$ that prevented us from estimating
373 nonlinear preferences in mean NDVI (i.e., the proxy for $E(R)$), since estimating the divers of
374 movement and disentangling them from potential confounds in a stochastic environemtn is
375 often complex or impossible (e.g., Wang et al. 2019). A tracking time series of two or more

³⁷⁶ years or additional individuals would have provided better estimates, but that was beyond
³⁷⁷ the scope of this empirical example.

³⁷⁸ **Conclusion**

³⁷⁹ The work presented here provides a unifying framework for viewing movement as a response
³⁸⁰ to resource abundance and stochasticity. We provide realistic and flexible hypotheses of the
³⁸¹ effects of $E(R)$ and $\text{Var}(R)$ on organisms' space-use requirements and movement behavior.
³⁸² We demonstrate that organisms' space-use requirements respond (*nonlinearly*) to both
³⁸³ resource abundance and stochasticity, and we demonstrate the importance of accounting for
³⁸⁴ $\text{Var}(R)$ besides $E(R)$.

³⁸⁵ *The hypotheses we presented here provide a framework of how one should*
³⁸⁶ *expect organisms to adapt their space use in response to changes in $E(R)$*
³⁸⁷ *and $\text{Var}(R)$. Similarly to the introduction of the Ideal Free Distribution by*
³⁸⁸ *Fretwell and Lucas (1969), the framework we present here allows one to de-*
³⁸⁹ *tect substantial deviations from the expected behavior and study the causes of*
³⁹⁰ *such deviations (e.g., Fretwell 2020). Recent advances in computation power*
³⁹¹ *have greatly increased analysts' ability to fit computationally demanding mod-*
³⁹² *els (Wood et al. 2017; Nathan et al. 2022), which allows (need a different*
³⁹³ *verb) biologists to move beyond only considering changes in mean conitions*
³⁹⁴ *and instead start thinking more about changes in the stochasticity of environ-*
³⁹⁵ *ments organisms live in, which is crucial in ecosystems of high and changing*
³⁹⁶ *stochasticity (Grant et al. 2017; Berger et al. 2018; Schmidt et al. 2020;*
³⁹⁷ *Rypkema and Tuljapurkar 2021; Yao et al. 2022; Intergovernmental Panel*
³⁹⁸ *On Climate Change 2023).*

³⁹⁹ **Conflict of interest**

⁴⁰⁰ The authors declare there are no conflicts of interest.

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