

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

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- make sure appendices flow (added stuff from main text)

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

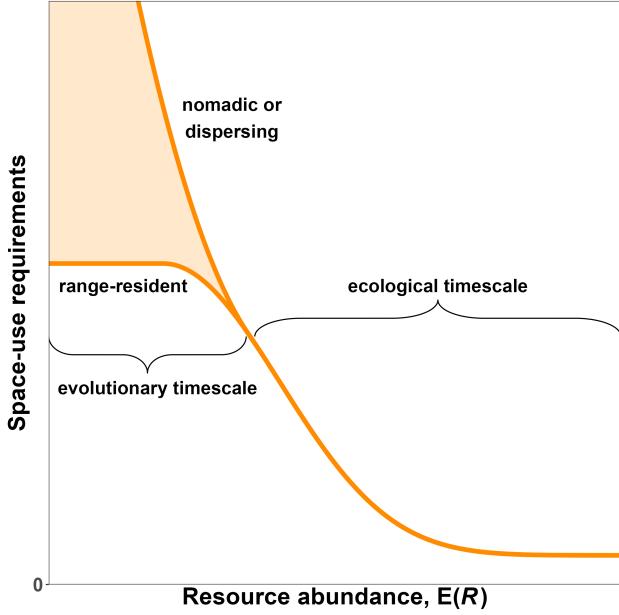


Figure 1: Hypothesized space-use requirements of an organism as a function of resource abundance ($E(R)$). We expect low values of $E(R)$ to result in high space-use requirements as organisms are forced to explore large areas to collect the resources they require to survive, whether they be range-resident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

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

179 We have provided the case for why both $E(R)$ and $\text{Var}(R)$ affect organisms' space-use require-
180 ments, but we presented the two parameters as independent drivers of movement. However,
181 in the more realistic scenario where both $E(R)$ and $\text{Var}(R)$ fluctuate over time, organ-
182 isms may respond to changes in $\text{Var}(R)$ more when resources are scarce than when they are
183 abundant. Consequently, models estimating the effects of R on organism's movement should
184 account for not only the effects of $E(R)$ and $\text{Var}(R)$ separately, but also their interactive

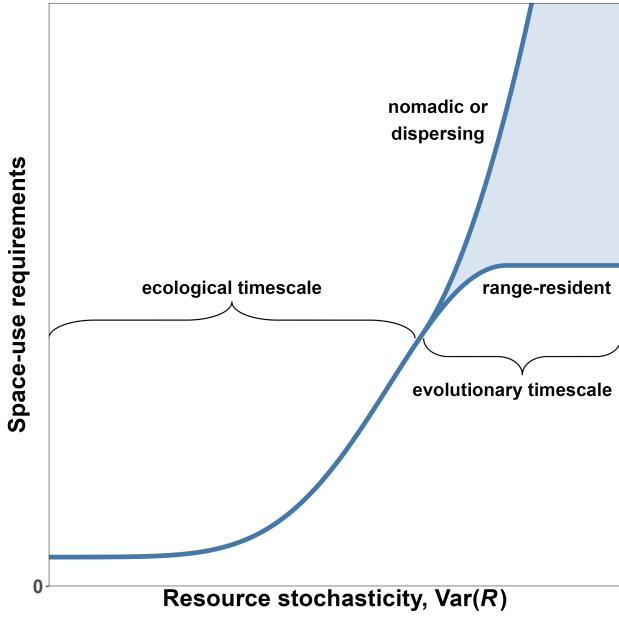


Figure 2: Hypothesized space-use requirements of an organism as a function of resource stochasticity ($\text{Var}(R)$). We expect low values of $\text{Var}(R)$ to result in low space-use requirements as organisms are able to depend on relatively predictable resources. As $\text{Var}(R)$ increases, space-use 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 effects. A highly unpredictable habitat may be very inhospitable if resources are poor, but
 186 $\text{Var}(R)$ may have little effect if resources are stochastic but always abundant. Thus, we
 187 expect $\text{Var}(R)$ to have a stronger effect on space-use requirements when $E(R)$ is low, and
 188 less of an effect when $E(R)$ is high.

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

190 To support our hypotheses of how organisms' space use is affected by $E(R)$, $\text{Var}(R)$, and the
 191 interaction effect of $E(R)$ and $\text{Var}(R)$, we present the results from a series of quantitative
 192 simulations. To start, we used the `ctmm` package (Fleming and Calabrese 2021) for `R` (`R`
 193 Core Team 2023) to generate 200 tracks (see Appendices 2 for sensitivity analyses) from an
 194 Integrated Ornstein-Uhlenbeck movement model [IOU model; Gurarie et al. (2017)]. The
 195 IOU model's correlated velocity produces realistic tracks with directional persistence despite
 196 the tracks being discrete samples of continuous-time movement processes. However, unlike

197 Ornstein-Uhlenbeck (OU) and Ornstein-Uhlenbeck Foraging (OUF) models, IOU models do
198 not assume the movement process is spatially stationary, so the organism is not assumed to
199 be range-resident. Consequently, each track is spatially unrestricted and can be interpreted
200 as purely exploratory movement.

201 Each of the 200 tracks were placed on a raster with common starting point $\langle 0, 0 \rangle$ and
202 sufficient time between tracks to be independent of one another (other than the starting
203 point). Each time the track moved to a new cell, the organism collected resources R sampled
204 from a Gamma distribution. The mean and variance of the distribution were defined by
205 deterministic functions $\mu(t)$ and $\sigma^2(t)$ (orange and blue lines in fig. 3). Note that t was
206 constant within each set of 200 tracks, so the time spent moving by the organism in each
207 track did not affect the distribution R was sampled from. Tracks were truncated once the
208 organism reached satiety, and the organism was given enough time to return to $\langle 0, 0 \rangle$ with no
209 correlation to the following track. Finally, each set of 200 truncated tracks was modeled using
210 an OUF model and Autocorrelated Kernel Density Estimate to estimate the 95% utilization
211 distribution. Additional information is provided in Appendix B.

212 Fig. 3 shows how the simulated space-use requirements changed in response to $\mu(t)$ and
213 $\sigma^2(t)$. The top row (constant $\text{Var}(R)$) shows how space-use requirements vary for different
214 trends in $\mu(t)$ while $\text{Var}(R)$ remains constant (like in fig. A1). As $E(R)$ increases at a constant
215 slope (linear $\mu(t)$) the space-use requirements decrease nonlinearly, with larger changes when
216 $E(R)$ is low, until home-range size approaches the minimum size required by the organism.
217 As described in the section on the effects of resource abundance, the nonlinear decrease is
218 because changes in $\mu(t)$ have a larger effect when $E(R)$ is low (e.g., Lucherini and Lovari
219 1996; Herfindal et al. 2005; Nilsen et al. 2005).

220 In regions where the $\mu(t)$ changes over time (e.g., seasonal changes – see cyclical $E(R)$
221 and Lai et al. 2017), organisms should have access to sufficient space to fulfill their needs
222 during periods of scarcity, whether the space available is sufficiently large year-round or it
223 changes seasonally with the expected changes in $\mu(t)$ (e.g., winter park closures). However,

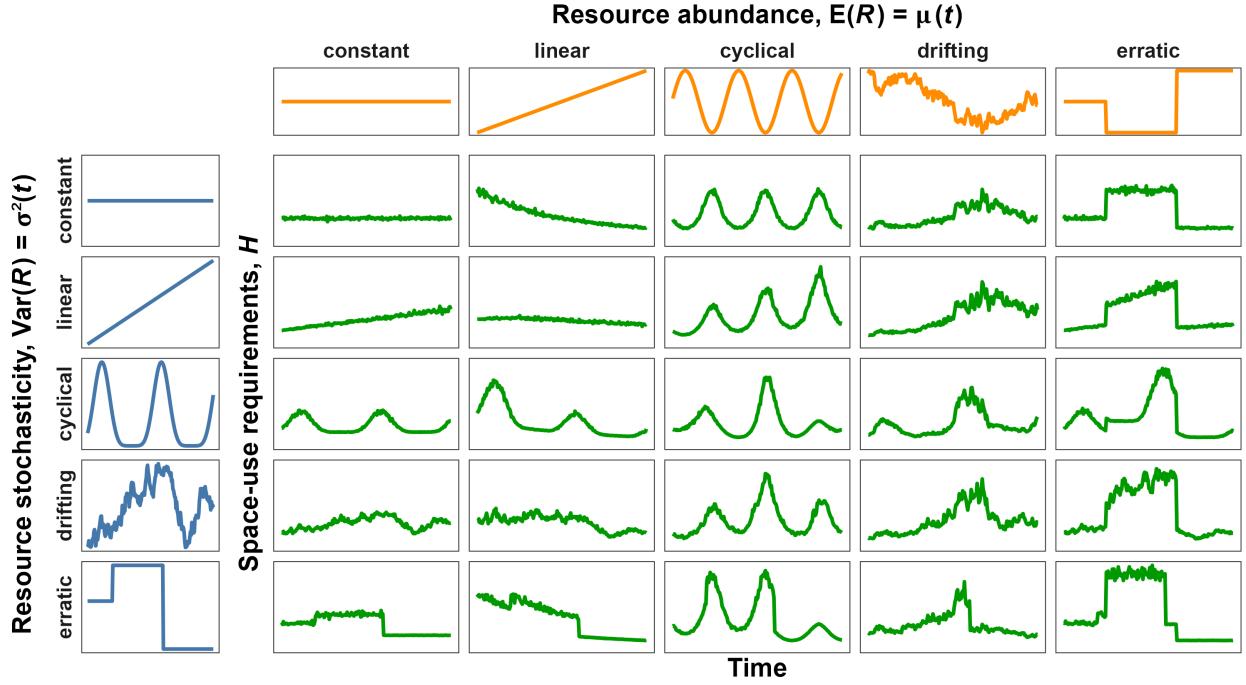


Figure 3: Simulated home range sizes, H , of an organism living in habitats where the mean and variance in resources are constant, linearly increasing, cyclical, drifting, or erratic over time (and homogenous over space). Note how H decreases nonlinearly as $\mu(t)$ increases and increases nonlinearly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

estimates of spatial requirements based on estimated changes in $\mu(t)$ should be interpreted carefully, since model error and unforeseeable decreases in $E(R)$ (such as following fires or floods) may increase organisms' space-use requirements suddenly and unpredictably. Thus, it is best to include a "buffer" area so the available space is larger than the estimated space-use requirements. This is particularly the case in environments where resource abundance changes unpredictably (drifting $\mu(t)$), since accurate long-term estimates and predictions of $\mu(t)$ may be hard to produce, if not impossible. In cases where $\mu(t)$ is highly unpredictable, organisms 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 $\mu(t)$).

The leftmost column of fig. 3 (constant $E(R)$) illustrates the effects of $\text{Var}(R)$ on the simulated space-use requirements while $E(R)$ remains constant. Overall, both mean H and the variance around it increase with $\sigma^2(t)$ (most visible with constant $E(R)$ and linear

237 $\text{Var}(R)$). This is because, similarly to resource-poor periods, times of greater stochasticity
238 require the organism to move over larger areas for longer periods of time. This results in a
239 greater uncertainty in how much time and space the organism will require to reach satiety, or
240 indeed whether an organism living in highly stochastic environments can even reach satiety
241 within a finite amount of time.

242 The remaining panels in fig. 3 illustrate how the effect of $\text{Var}(R)$ depends on $E(R)$
243 (and vice-versa) as well as how complex the relationship can be. Since $E(R)$ and $\text{Var}(R)$
244 have opposite effects on H , disentangling the effects can be particularly difficult when both
245 parameters change in a correlated manner (e.g., linear $E(R)$ and $\text{Var}(R)$). When both $E(R)$
246 and $\text{Var}(R)$ increase linearly, H initially increases since the effect of $\text{Var}(R)$ is stronger, but
247 then decreases as the effect of $E(R)$ begins to dominate. However, when $\mu(t)$ and $\sigma^2(t)$
248 follow fairly different trends (e.g., cyclical $E(R)$ and linear $\text{Var}(R)$), it is easy to see how an
249 increase in $\text{Var}(R)$ amplifies the effects of $E(R)$. In contrast, the effect of $\text{Var}(R)$ is stronger
250 when $E(R)$ is low (e.g., linear $E(R)$ with cyclical $\text{Var}(R)$). Thus, H is largest when $E(R)$
251 is low and $\text{Var}(R)$ is high, and it is smallest when $E(R)$ is high and $\text{Var}(R)$ is low (see the
252 panel with cyclical $E(R)$ and $\text{Var}(R)$ as well as Lai et al. 2017).

253 Not all 25 scenarios depicted in fig. 3 may be realistic, but the trends in $E(R)$ and
254 $\text{Var}(R)$, and their impacts on space use are useful examples that can be thought of as
255 simplified scenarios. $E(R)$ and $\text{Var}(R)$ may be assumed to be (approximately) constant in
256 highly homogeneous environments. Although it is impossible for $\mu(t)$ and $\sigma^2(t)$ to increase
257 linearly forever, these examples are useful to demonstrate that linear changes in $\mu(t)$ and
258 $\sigma^2(t)$ affect H nonlinearly. Cyclical oscillations in $E(R)$ and $\text{Var}(R)$ may occur in urban
259 environments as human activity changes within and between days (Péron et al. 2017; Ikeda
260 et al. 2022) and as temperatures fluctuate daily and seasonally (Geremia et al. 2019; Alston
261 et al. 2020), while $E(R)$ and $\text{Var}(R)$ may drift randomly in highly complex environments
262 which are too hard to predict. Finally, erratic changes in $E(R)$ and $\text{Var}(R)$ may occur in
263 environments where changes are very sudden, such as areas prone to fires or floods, as well

264 as habitats with drastic human alteration (e.g., a forest which is clear-cut with a subsequent
265 artificial re-forestation). However, if stochastic changes are sufficiently small and frequent,
266 organisms may perceive them as continuous and smooth changes rather a series of small and
267 sudden changes.

268 Although the temporal trends in fig. 3 are complex and the effects of $E(R)$ and $\text{Var}(R)$ can
269 be hard to disentangle, two surprisingly simple relationships emerge when home-range size is
270 shown as a function of either $E(R)$ or $\text{Var}(R)$, rather than time. Both $E(R)$ and $\text{Var}(R)$ affect
271 space-use requirements precisely as we hypothesized (fig. 4). We believe the approximately
272 linear effect of $\text{Var}(R)$ on H is mainly due to two factors. Firstly, H scales superlinearly with
273 the standard deviation in R (as $\sqrt{\text{Var}(R)}$ is on the same scale as $E(R)$; not shown), which
274 would necessarily imply that H increases sublinearly with $\text{Var}(R)$. Secondly, the organism's
275 movement was simulated to be range resident within an homogeneous environment. Since
276 real-world landscapes are spatially heterogeneous in both $E(R)$ and $\text{Var}(R)$, organisms may
277 choose to shift their home range to a new area following a stochastic event that caused $\mu(t)$
278 to decrease, such as a fire or a flood. Thus, we hypothesize that our simulations may be
279 underestimating organisms' responses to spatiotemporal changes in $E(R)$ and $\text{Var}(R)$, since
280 the simulated organisms cannot select for areas of higher $E(R)$ or lower $\text{Var}(R)$. Additionally,
281 the simulations also ignore how competition, movement costs, predation, and other factors
282 may affect the effects of $E(R)$ and $\text{Var}(R)$ on H . While these are definitely important effects
283 that should be accounted for (Jetz et al. 2004), doing so was beyond the scope of this paper.

- 284 • Effects of $\mu(t)$ and $\sigma^2(t)$ on $\text{Var}(R)$.

285 Applying the framework

286 In this section, we show how this framework can be applied to better understand the move-
287 ment ecology of free-ranging organisms via remote sensing data such as NDVI (Pettorelli
288 et al. 2011). To illustrate the methods, we use empirical tracking data on a lowland tapir

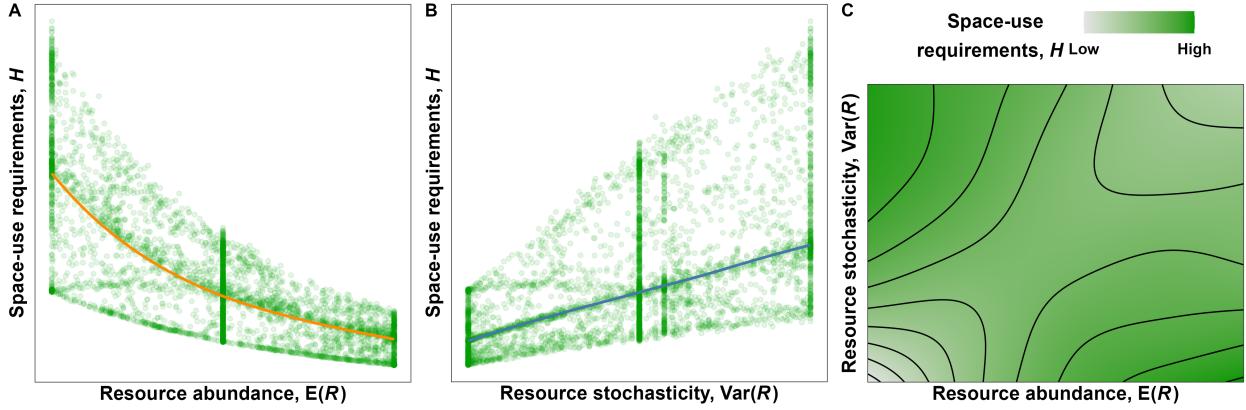


Figure 4: Effects of $E(R)$ and $\text{Var}(R)$ on simulated spatial requirements with 95% credible intervals for the mean (overlapping the line). Credible intervals were calculated assuming a gaussian posterior distribution on the link scale. The relationships were estimated using a Generalized Additive Model for Location and Scale (GAMLS; Rigby and Stasinopoulos 2005; Stasinopoulos and Rigby 2007) with a Gamma location-scale family of distributions (`mgcv::gammals`). The model accounted for the effects of $E(R)$ and $\text{Var}(R)$ and the interaction effects between the two on both the location (i.e., mean) of H and its scale parameter. Note the nonlinear decrease in H as $E(R)$ increases and the increase in H as $\text{Var}(R)$ increases. Additionally, note how the variance in space-use requirements strongly increases with mean space-use requirements.

from the Brazilian Cerrado. 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.

The hypotheses we present here allow researchers to combine otherwise complicated findings (e.g., fig. 3) and generalize results to a single, common set of functions. We expect the two hypotheses we present here (figs. 1 and 2) to be applicable to all motile organisms, once differences in size, metabolic needs, and diet are accounted for. In this subsection, we illustrate how researchers can leverage these hypotheses using their own data to build on previous work rather than listing the results as new findings. Additionally, the analyses can be expanded to the population or species level with the use of Hierarchical Generalized Additive Models (HGAMs) with individual-level intercepts and smooth terms (see models “GS” and “GI” in Pedersen et al. 2019). Such models would allow one to test whether members of the same population or species respond similarly to $E(R)$ and $\text{Var}(R)$ while also quantifying any deviation from the hypothesized behavior. Individuals and populations that

were once thought to have different space-use requirements due to differences in behavior
may instead be simply responding to different local conditions along the functions in figs. 1
and 2 (e.g., Singh et al. 2012). In the following sections, we illustrate how one can apply
this framework to empirical data.

We start by providing examples and considerations on how one may model R and the
effects of $E(R)$ and $\text{Var}(R)$ on organisms' space-use requirements. Next, we apply the
methods to the tapir's GPS tracking data and use 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 organisms' space-use requirements under
different scenarios.

Modeling R

Location-scale models (Rigby and Stasinopoulos 2005; Stasinopoulos and Rigby 2007) are
a class of statistical models that allow us to estimate changes in a random variable's mean
(i.e. its location) and variance (which depends on its scale) while allowing the mean-variance
relationship to vary. `mgcv` (Wood 2017) is a commonly used package for R (R Core Team
2023) that allows one to fit Generalized Linear Models (GLMs, see Zuur 2009) and Gener-
alized Additive Models (GAMs, see Wood 2017), including hierarchical and location-scale
GLMs and GAMs. Currently, the `mgcv` package allows one to fit location-scale models with
various families of distributions, including Gaussian (i.e., normal), gamma, and Tweedie
location-scale families.

The Gaussian location-scale family of distributions is very flexible, since the mean and
variance parameters are assumed to be independent, and the response can be either positive
or negative. However, the distribution's flexibility can also result in unreliable estimates for
non-Gaussian responses, such as strictly positive data (e.g. available biomass), count data
(e.g., number of prey), proportions (e.g., percentage of forested habitat), and bounded ratios
(e.g., NDVI, see Pettorelli et al. 2011).

331 The Gamma location-scale family is best for strictly positive responses, such as areas
332 (including home ranges), elemental compositions (e.g., carbon to nitrogen ratio, see Rizzuto
333 et al. 2021), total biomass, or energetic intake. The Tweedie location-scale family is similar
334 to the Gamma family, but it allows for zero data, so it is appropriate for data with a non-
335 trivial amount of zeros, such as daily precipitation or prey density (but see zero-inflated
336 distributions: Zuur et al. 2009). In this paper, we estimate R by modeling NDVI using `mgcv`
337 and a beta location-scale family (not available in `mgcv` at the time of publication). If one
338 is interested in families of distributions which are not available in `mgcv`, we suggest using
339 the `brms` package (Bürkner 2017), which allows full control over all of a family's parameters
340 via a fully Bayesian approach (as opposed to `mgcv`'s Empirical Bayes method – see Bürkner
341 2018).

342 Modeling the mean and variance terms of R should be done carefully. Since trends in
343 both $E(R)$ and $\text{Var}(R)$ can be spatiotemporally nonlinear and non-monotonic, we suggest
344 using a GAM rather than a GLM. However, the complexity of the spatiotemporal terms
345 should be chosen carefully, particularly for the mean's terms. An excessively wiggly $\hat{\mu}(t)$
346 will cause $\sigma^2(t)$ to be under-estimated, while an excessively smooth $\hat{\mu}(t)$ will cause $\sigma^2(t)$ to
347 be over-estimated. Although there is no error-proof system, choosing the complexity of the
348 terms based on the organism's ability to detect change and adapt is a reasonable starting
349 point. Additionally, setting the basis dimension (k) of the scale terms to be half or less than
350 that of the mean terms and using restricted marginal likelihood (Wood 2011) should provide
351 reasonably accurate results. We suggest starting with low values of k and adjusting k based
352 on the trends in the residuals. Note that since R is likely spatiotemporally autocorrelated,
353 it may be easy to overfit the model. Simpson (2018) provides a useful introduction to GAMs
354 for biological time series.

355 **Estimating R using NDVI**

356 Since there is no commonly-used distribution with a support over the interval $[-1, 1]$, we
 357 use beta distribution after scaling NDVI to the interval $[0, 1]$ by applying the linear trans-
 358 formation

$$\nu_{[0,1]} = \frac{\nu + 1}{2}, \quad (2)$$

359 where ν indicates the NDVI value in $[-1, 1]$ and $\nu_{[0,1]}$ is the scaled NDVI value (see Denny
 360 2017 for more information on transforming response data). In this case, we can define R as
 361 following a beta distribution with mean and variance that depend on time using the notation
 362 $B(\mu(t), \sigma^2(t))$. We use this parameterization here for ease of explanation, but note that beta
 363 distributions are generally parameterized using the shape parameters α and β such that the
 364 mean is

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

365 while the variance is

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

366 We can easily convert $\mu(t)$ and $\sigma^2(t)$ back to mean and variance in NDVI using the inverse
 367 of equation (2):

$$\nu = 2\nu_{[0,1]} - 1. \quad (5)$$

368 Consequently, we have

$$E(\nu|t) = 2\mu(t) - 1. \quad (6)$$

369 and

$$\text{Var}(\nu|t) = 2^2\sigma^2(t) + 0 = 4\sigma^2(t). \quad (7)$$

370 Particular attention should be given when deciding what distribution to use and
371 how to estimate means and variances in R . Improper models and simulations of resource
372 abundance can fail to produce robust, sensible, and accurate estimates of R .

373 Modeling the effects of $E(R)$ and $\text{Var}(R)$ on space-use requirements

374 As discussed in the previous section, the first step to modeling H is to choose an appropriate
375 family of distributions. Since H is strictly positive and continuous, a Gamma family seems
376 the most appropriate among the distributions currently offered by the `mgcv` package (Wood
377 2017), but the Tweedie family would also be appropriate if the variance does not scale with
378 the squared mean.

379 As with the simulated effects of $\mu(t)$ and $\sigma^2(t)$ on H (fig. 4), a location-scale Gamma
380 model is likely required. If there is not sufficient data to fit a location-scale model (which is
381 not the case here), a simple Gamma model may be sufficient, but we suggest selecting the
382 best family of distributions using an information criterion such as the Akaike Information
383 Criterion (Akaike 1974). Due to potential correlation between $E(R)$ and $\text{Var}(R)$ in a small
384 and autocorrelated sample, the relationship between R and H should be modeled carefully
385 and with parsimony. Below, we present an empirical example using GPS tracking data from
386 a lowland tapir (*Tapirus terrestris*) and satellite-derived NDVI. Additional information can
387 be found in Appendix C.

388 The effects of $E(R)$ and $\text{Var}(R)$ on a lowland tapir's space-use requirements

389 Fig. 5 illustrates how a tapir in the Brazilian Cerrado (data from Medici et al. 2022) adapts
390 its spatial needs to changes in $E(R)$ and $\text{Var}(R)$. Panels A and B show the changes in
391 seven-day average mean and variance in NDVI, respectively, experienced by the tapir during
392 the tracking period. Panel C shows the changes in the tapir's 7-day home range over time.
393 Note how the tapir uses more space during periods of lower NDVI (e.g., August 2017) and
394 less space during periods with high NDVI (January 2018). Additionally, when resources are

395 scarce and highly unpredictable (August 2018), the tapir uses up to 5 times more space than
396 when resources are abundant and predictable (e.g., January 2018). Finally, panels D and E
397 show the estimated (marginal) effects of $\mu(t)$ and $\sigma^2(t)$ on the tapir's space use. Since $\mu(t)$
398 and $\sigma^2(t)$ are strongly correlated (panel F) and (spatio)temporally autocorrelated (panels A
399 and B), the effects of R on H should be modeled carefully. To avoid over-fitting the model,
400 we constrain the smooth effects of $\mu(t)$ and $\sigma^2(t)$ using a shape-constrained additive models
401 (SCAM) with monotone decreasing and increasing P-splines for $\mu(t)$ and $\sigma^2(t)$, respectively.

402 Modeling the tapir's space use as a function of resource abundance alone would result
403 in an excessively strong estimated effect and a worse model fit ($\Delta\text{AIC} \approx 87$, see Appendix
404 C). By including the effect of $\sigma^2(t)$ in the model along with that of $\mu(t)$, we show that the
405 tapir responds to both resource abundance and stochasticity. While the tracking period may
406 be too short to see the effects of $E(R)$ clearly, it should also be noted that the Cerrado is
407 relatively rich in vegetation throughout the entire year (fig. 5A), and thus the tapir does
408 not experience resource scarcity during the tracking period. Consequently, this example
409 demonstrates two points central to this paper. Firstly, even animals in resource-rich regions
410 such as the Brazilian Cerrado adapt their behavior in response to resource stochasticity.
411 Secondly, trends in mean resources alone are not sufficient to explain the tapir's space use,
412 and the stochasticity in R is an important driver of the tapir's movement.

413 Discussion

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

415 Paragraphs to tie in:

- 416 • It is also worth noting that high $E(R)$ does not necessarily imply that organ-
417 isms have access to high amounts of resources, as predator avoidance and competition
418 within an organism's habitat will decrease the proportion of R it is able to access.
419 Thus, organisms in habitats with strong competitive pressure and predation may re-

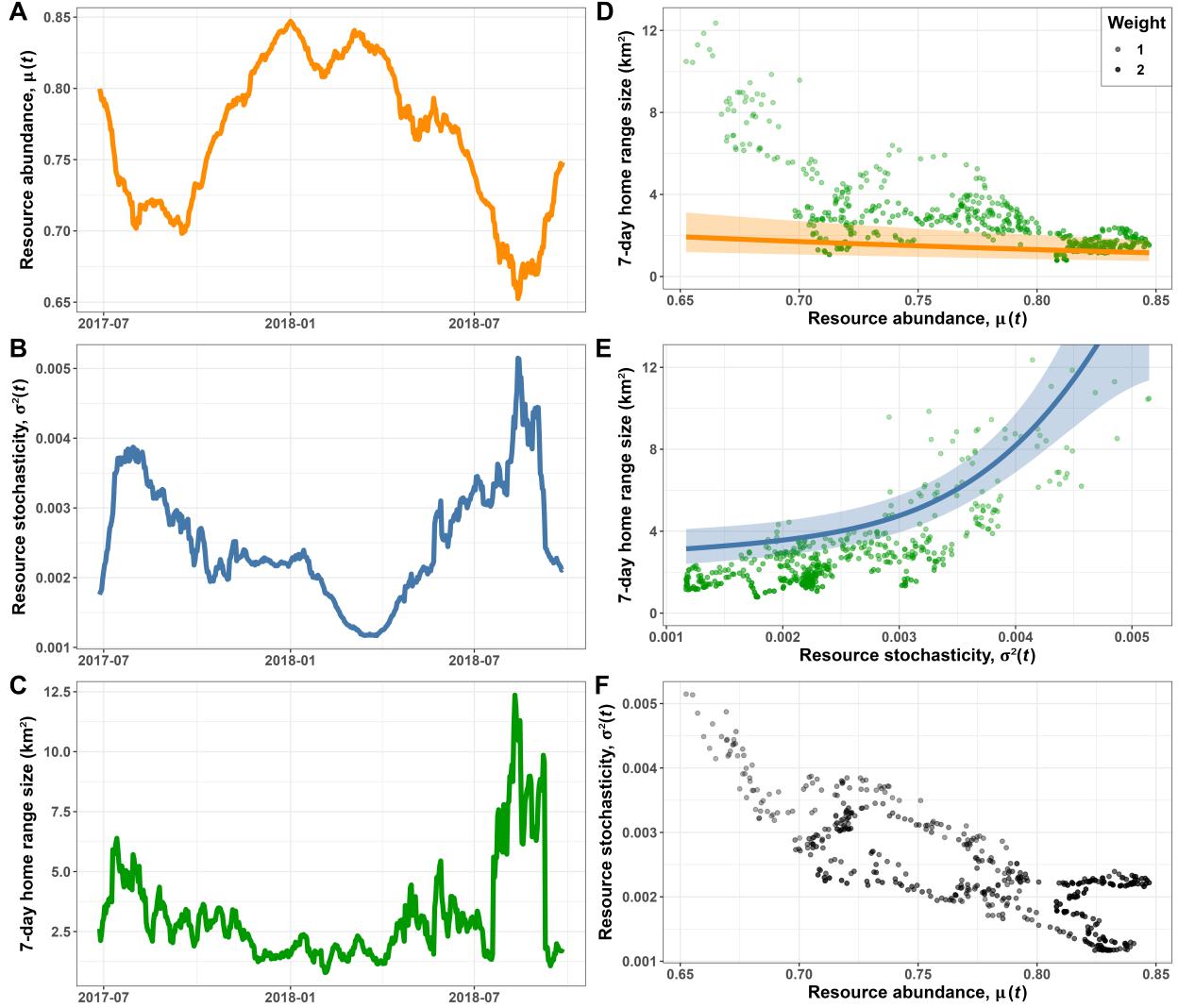


Figure 5: Seven-day home-range size of a lowland tapir (*Tapirus terrestris*) in response to changes in mean and variance in resources. (A) Trends in resource abundance over time, $\mu(t)$, estimated as the average mean NDVI at the locations visited by the tapir during a seven-day period. (B) Variance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

420 quire larger home ranges (Jetz et al. 2004; Prox and Farine 2020), but larger home
421 ranges can be harder to defend and also result in higher rates of competition and
422 movement costs (Grant 1993; Jetz et al. 2004; but also see Dickie et al. 2022). Ad-
423 ditionally, persistent territorial defense from competitors may prevent organisms from
424 using space freely and as necessary (wolves, *Canis lupus*: Rich et al. 2012; feral cats,
425 *Felis catus*: Bengsen et al. 2016; Capuchin monkeys, *Cebus capucinus*: Tórrez-Herrera
426 et al. 2020), so the effect of $E(R)$ on space use may vary between individuals, species,
427 and locations. Still, these pressures simply alter the intensity with which organisms
428 respond to $E(R)$ but not the shape of the relationship, since each of these cases fall
429 along different parts of the continuum in $E(R)$ shown in fig. 1.

- 430 • Rizzuto et al. (2021) found that the space-use requirements of snowshoe hares (*Lepus*
431 *americanus*) increased with average carbon to nitrogen ratio (C:N, a measure of N
432 scarcity) in lowbush blueberry as well as the coefficient of variation (the standard
433 deviation divided by the mean, $\frac{\sqrt{\sigma^2(t)}}{\mu(t)}$) in C:N. However, it is hard to determine how
434 $\sigma^2(t)$ affected the hares' space-use requirements since the coefficient of variation is a
435 function of both $\mu(t)$ and $\sigma^2(t)$, so the effects of the two variables are confounded.
436 Similarly, Mueller et al. (2011) suggested that ecosystem variability [measured as
437 spatial semivariance in Normalized Difference Vegetation Index, NDVI; see Pettorelli
438 et al. (2011)] causes ungulates to move more and adopt more nomadic behaviors, but it
439 is hard to determine whether the higher semivariances in NDVI are due to an increase in
440 $Var(R)$ or simply spatial changes in $E(R)$ (e.g., increased seasonality or continentality).
441 Likewise, Herfindal et al. (2005) found that the home ranges of Canadian lynx (*Lynx*
442 *canadensis*) decreased with seasonality, but this may be an artifact of a lower $\mu(t)$ in
443 highly seasonal environments, rather than stochasticity in R . A subsequent analysis
444 by Nilsen et al. (2005) of the lynx data of Herfindal et al. (2005) along with data on
445 wolverines (*Gulo gulo*), bobcats (*Lynx rufus*), and coyotes (*Canis latrans*) found that
446 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 novel situations and increasingly common and extreme stochastic events (Noonan et al. 2018; Yao et al. 2022; Intergovernmental Panel On Climate Change 2023).

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

The spatiotemporal scale over which an event occurs is a main determinant of whether an organism will be able to predict the event and how it will respond to it (or fail to do so). Events that occur at the scale of the organism (i.e. approximately one or more times per generation and on the spatial scale of the organism's spatial range, see Frankham and Brook 2004) are more likely to be perceived as a threat or boon worth preparing for (Foley et al. 2008; Berger et al. 2018; Geremia et al. 2019). Consequently, organisms with long

generations (e.g., elephants, *Loxodonta sp.*) or large spatial ranges (e.g., migratory birds) are more likely to experience stochastic events and thus are also more likely to respond to and prepare for them. Animals may adapt by adjusting the timing of reproduction (Southwood 1977; Boersma et al. 2021) and torpor or hibernation (Inouye et al. 2000; Goldberg and Conway 2021), or storing large amounts of energy (Lindstedt and Boyce 1985) through fat storage (Armitage et al. 2003; Nespolo et al. 2022) or resource caching (Post et al. 2006). Alternatively, animals may alter their movement and travel long distances over short periods of time (Jetz et al. 2004; Hirt et al. 2017), whether this be for migration (Mueller et al. 2013; Geremia et al. 2019) or nomadism (Teitelbaum et al. 2015; Nandintsetseg et al. 2019; Teitelbaum and Mueller 2019). Over the years, animals may also develop more complex cognitive abilities (Brown et al. 2004), including the development of memory (Foley et al. 2008; Fagan et al. 2013; Polansky et al. 2015; Abrahms et al. 2019; Geremia et al. 2019; Rickbeil et al. 2019; Riotte-Lambert and Matthiopoulos 2020; Steixner-Kumar and Gläscher 2020; Falcón-Cortés et al. 2021; Cavedon et al. 2022; Ranc et al. 2022), which is required for migration (Mueller et al. 2013; Middleton et al. 2018; Abrahms et al. 2019; Geremia et al. 2019; Merkle et al. 2019; Rickbeil et al. 2019; but see: Cuadrado 2021; Stefanescu et al. 2021). However, adapting to changes in environmental cues rather than relying on memory alone (Jonzén et al. 2006; Büntgen et al. 2017; Rickbeil et al. 2019; Severson et al. 2021), can prevent animals from becoming trapped in sub-optimal conditions (Abrahms et al. 2019).

In contrast, individuals with short lifespans are less likely to experience stochastic events and develop memory about them. However, the short generation time and high reproductive rate of r-selected species (as opposed to k-selected species, see Pianka 1970; Brown et al. 2004) may promote other traits that increase survival following extreme events. Examples include higher population size, dispersal, higher genetic diversity, and complex group dynamics (e.g., Cuadrado 2021; Stefanescu et al. 2021). Events that occur over large spatiotemporal scales can thus promote slow, large-scale changes through the adaptation, natural selection,

and evolution of the species (Gienapp et al. 2008; Logares and Nuñez 2012; Anderson et al. 2017; Grant et al. 2017), which is more likely to adapt if starting populations are large with high genetic diversity and short generations, as in the case of r-selected species (but see Leung 2022). Of course, an organism with a lifespan shorter than a year will be unable to experience the cyclical nature of the seasons, and an organism with a lifespan of a few weeks or days may not even experience substantial changes in weather other than daily cycles and some weather stochasticity. Still, a population may respond to spatiotemporal cycles in $E(R)$ and $\text{Var}(R)$ by adapting the group's reproduction timing and migration (e.g., painted lady butterflies: Cuadrado 2021; Stefanescu et al. 2021).

A population's fitness and chances of survival in a changing environment depend strongly on its adaptability and responsiveness to change (Riotte-Lambert and Matthiopoulos 2020), and its ability to recognize cues that precede extreme events or periods of scarcity or abundance can have appreciable effects on its members' chances of survival and reproduction. For example, ungulates' ability to time their yearly migrations on available forage biomass, snow fall, snow melt, and hunting pressure allow them to adapt to changes in both $E(R)$ and $\text{Var}(R)$, while their spatial memory (Falcón-Cortés et al. 2021; Ranc et al. 2022) allows them to optimize their large-scale movement by reducing the amount of time and energy spent exploring. Similarly, the ability of trans-Saharan migrant birds to adapt their migration timing based on environmental cues allows them to account for differences in $\mu(t)$ between years (Jonzén et al. 2006). However, relying too strongly on short-term changes rather than depending on long-term memory can also cause animals to fail to find crucial resources during unpredictable times (whooping cranes: Mueller et al. 2013; Foley et al. 2008; elephants: Polansky et al. 2015; whales: Abrahms et al. 2019). Instead, if anomalies occur repeatedly over time, organisms may adapt to a higher $\sigma^2(t)$ or shift their ranges altogether (terrestrial animals: Chen et al. 2011; Büntgen et al. 2017; ungulates: Severson et al. 2021), including migratory animals (Jonzén et al. 2006). Still, while range shifts can help species overcome changes in the long-term trends in $\mu(t)$ and $\sigma^2(t)$, including changes in phenology (Severson

528 et al. 2021), they can also result in phenological mismatches (Lameris et al. 2018) and add
529 pressure to the species that already live in the habitat (e.g., Wallingford et al. 2020; but see
530 Shepard et al. 2022), including specialists and obligate symbionts that may be unable to
531 shift their range, since it is determined by their food sources' and associates' ability to move
532 and adapt, too.

533 Applications for conservation

534 Technical advancements from the last few decades have allowed scientists to collect increas-
535 ingly larger amounts of data at finer and finer scales (Nathan et al. 2022), but little at-
536 tention has been paid to estimating the effects of environmental stochasticity on organisms'
537 behaviors. In these times of great change and climatic uncertainty (Abrahms 2021; Inter-
538 governmental Panel On Climate Change 2023), it is increasingly important to recognize how
539 environmental stochasticity affects organisms' behaviors and shapes ecosystems. Accounting
540 for changes in both resource abundance and resource stochasticity is crucial when assessing
541 whether the quality of protected areas is sufficiently high to sustain biodiversity long term.
542 Protecting areas with high resource abundance and low resource stochasticity will reduce
543 animals' spatial requirements.

544 The designation of high-quality habitats is a central concern of many conservation initia-
545 tives. This framework allows consultants and conservation managers to quantify the quality
546 of a habitat based on its resource abundance and stochasticity as well as the amount of
547 space animals would need in the habitat. With the methods presented in this paper, one
548 can (1) assess the quality of current protected areas, (2) predict whether or not the areas
549 will be able to sustain current populations in future decades, and (3) evaluate the quality of
550 new potential conservation areas. In light of the UN's objective to conserve 30% of global
551 landmasses and waters by 2030 (IPBES 2019), the framework and methods presented here
552 provide useful metrics for evaluating whether protected areas will have sufficient quality
553 and long-term stability to support species under various possible climate change scenarios

554 (Intergovernmental Panel On Climate Change 2023).

555 Ignoring the effects of recent and predicted increases in $\text{Var}(R)$, including an increase
556 in the intensity and frequency of extreme events (Yao et al. 2022; Intergovernmental Panel
557 On Climate Change 2023), has the potential to greatly hinder future conservation efforts.
558 Since not accounting for an increase in $\sigma^2(t)$ will result in an under-estimation of animals'
559 space-use requirements, protected areas which were designated based on the area's $\mu(t)$ but
560 not $\sigma^2(t)$ will likely be insufficient in both size and resources in the future, which may lead to
561 decreases in the fitness and size of a population while also increasing the risk of population
562 collapse and human-wildlife conflict (Mukeka et al. 2019). This is particularly the case
563 in resource-poor, stochastic regions, where animals are forced to endure longer and more
564 unpredictable searches, which results in a larger variance in space-use requirements.

565 It is also worth noting that carnivores may be more susceptible to changes in $E(R)$ and
566 $\text{Var}(R)$, and that this susceptibility is likely amplified further at higher trophic levels. While
567 primary consumers can rely on relatively predictable and static resources that can be esti-
568 mated easily via remote sensing measures such as NDVI, the fine-scale location of secondary
569 consumers' resources may not correlate as strongly with measures of habitat productivity. In
570 fact, primary consumers' ability to move makes their location and abundance more stochas-
571 tic than those of plants. Consequently, the abundance of primary consumers may correlate
572 with productivity weakly or at a temporal lag (e.g., Geremia et al. 2019). Thus, primary
573 consumers' delayed responses to fluctuations in $E(R)$ and $\text{Var}(R)$ may result in an increase
574 in secondary consumers' resource stochasticity, which would also be perceived with a delay.
575 Similar hypotheses can be formulated for higher trophic levels but with amplified temporal
576 lags, since each trophic level adds another layer of uncertainty and delayed response, which
577 together increase the unpredictability on how carnivores indirectly respond to changes in
578 primary productivity. However, the effect is likely less pronounced for omnivores and other
579 diet generalists, as they may have the ability to switch to more abundant and less stochastic
580 resources.

581 **Conclusion**

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

594 **Conflict of interest**

595 The authors declare there are no conflicts of interest.

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