

How resource abundance and stochasticity affect organisms' range sizes

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1 Abstract

2 The amount of space organisms use is thought to be tightly linked to the availability of
3 resources within their habitats, such that organisms living in productive habitats generally
4 require less space than those in resource-poor habitats. This hypothesis has widespread em-
5 pirical support, but existing studies have focused primarily on responses to the mean amount
6 of resources, while responses to the variance around the mean are still largely unknown. This
7 is not a trivial oversight. Organisms adjust to variable environmental conditions, so failing
8 to consider the effects of resource (un)predictability can result in a limited understanding
9 of an organism's range size, which challenges 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 range sizes. Next, we use
12 simulated movement data to demonstrate how the combined effects of mean and variance
13 in resource abundance interact to shape predictable patterns in range size. Finally, we use
14 real-world tracking data on a lowland tapir (*Tapirus terrestris*) from the Brazilian Cerrado
15 to show how this framework can be applied to better understand the movement ecology of
16 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 al.
²⁴ 2008; Berger et al. 2018). Thus, many organisms adapt their behaviors and/or physiology
²⁵ in response to changes in local resource abundance to ensure their needs are met.

²⁶ While there are many ways that individuals can respond to resource availability, move-
²⁷ ment represents one of the most readily available traits that species can adjust (Charnov
²⁸ 1976; Kacelnik et al. 1992). The relationship between organisms' movement and resource
²⁹ abundance has long been of interest to biologists. In his seminal paper, Burt (1943) con-
³⁰sidered the search for food as the primary driver for movement within an organism's home
³¹ range. Three decades after, Southwood (1977) suggested that change in resource abundance
³² drives how organisms decide where to live and when to reproduce. Two years later, Harestad
³³ and Bunnel (1979) proposed that the simplest relationship between resource abundance and
³⁴ an organism's home-range size is

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

³⁵ where H is the organism's home-range size, C is the organism's resource consumption (kcal
³⁶ day^{-1}), and R is the resources the organism can access ($\text{kcal day}^{-1} \text{ unit area}^{-1}$). Harestad
³⁷ and Bunnel's model is simple to conceptualize, and it allows for testable predictions, but few
³⁸ studies are structured around a set of theoretical expectations such as Harestad and Bunnel's
³⁹ hypothesis. Many researchers have since demonstrated that organisms adapt their range sizes
⁴⁰ in response to resources abundance, but results are typically reported as independent, novel

41 findings. Perhaps more problematic is the fact that, while much work has been done on
42 estimating organisms' responses to mean resource abundance, there is little information on
43 how organisms respond to variance around the mean (i.e., resource stochasticity, but see:
44 Stephens and Charnov 1982; Duncan et al. 2015; Rizzuto et al. 2021). Thus, there remains
45 a need for a clear hypothesis for the effects of both resource abundance and stochasticity on
46 organisms' range sizes.

47 Here, we refer to a location's average amount of resources as "resource abundance",
48 while we use the phrase "resource stochasticity" to indicate the variability in resources af-
49 ter accounting for changes in the mean. We argue that, on its own, a habitat's resource
50 abundance is not sufficient to assess the habitat's quality, nor make predictions about how
51 much space an organism might use. To see this, consider,, for instance, a herbivore graz-
52 ing in a grassland with relatively low but constant forage availability (i.e., low mean and
53 variance). This individual will adopt a different behavior and adaptations if it lived in a
54 desert with equally scarce forage but rare, sudden, and strong pulses of resources (i.e., low
55 mean and high stochasticity). Although these two habitats may have the same long-term
56 average resource abundance, the ephemerality of resources in the stochastic desert environ-
57 ment would promote a different selection of movement and life history strategies. In the
58 grassland, the grazer may require a large but constant home range size as it moves between
59 patches in search of food, while in the desert it may switch between dispersal in search for
60 high-resource patches and short-term range residency within patches (*sensu* Charnov 1976;
61 see Singh et al. 2012; Wheat et al. 2017; Teitelbaum and Mueller 2019). Previous studies
62 suggest that resource stochasticity may decrease organisms' fitness and landscapes' energetic
63 balances (e.g., Chevin et al. 2010), but there is still limited empirical evidence to support
64 this hypothesis (but see: Herfindal et al. 2005; Nilsen et al. 2005; Rizzuto et al. 2021).

65 In this paper, we illustrate how an organism's range size can be expected to depend on
66 both the abundance and unpredictability of resources. First, we set the theoretical back-
67 ground necessary for the successive sections by introducing key concepts and notation. Next,

68 we provide a review of the effects of resource abundance on range sizes while suggesting a
69 simple and unifying hypothesis. Afterwards, we provide a review of the effects of resource
70 stochasticity on organisms' range sizes while suggesting a second simple and unifying hypoth-
71 esis. Subsequently, we support the two hypotheses using quantitative, simulated responses
72 in range size to changes in resource abundance and stochasticity. Finally, we demonstrate
73 how this framework can be used in practice to describe the movement ecology of a lowland
74 tapir (*Tapirus terrestris*) from the Brazilian Cerrado (Medici et al. 2022). Results from the
75 simulations and empirical example are presented using a fully transparent approach that
76 allows researchers to replicate the work and apply the methods to their own tracking data.

77 Resources as a random variable

78 Resources are often unpredictable (and difficult to quantify), since they depend on various
79 factors which cannot be accounted for easily, including climate (Lindstedt and Boyce 1985;
80 Morellet et al. 2013; Schmidt et al. 2020), weather (Morellet et al. 2013; Fjelldal et al.
81 2021), competitive pressure (Rich et al. 2012; Tórrez-Herrera et al. 2020), and differences in
82 energetics among individuals (Schmidt et al. 2020) and species (Jetz et al. 2004). Thus,
83 we can treat the amount of resources R at a given point in time (t) and space (location vector
84 \vec{u}) as a random variable, denoted as $R(t, \vec{u})$. Treating resources as a random variable allows
85 us to leverage techniques from probability theory and statistics, such as the expectation of a
86 random variable (i.e., its mean) and its variance around the mean. We indicate the expected
87 value and variance of random variable R using $E(R)$ and $\text{Var}(R)$, respectively, and we use
88 $\mu(t, \vec{u})$ and $\sigma^2(t, \vec{u})$ to indicate them as functions of time (t) and space (\vec{u}). Additional
89 definitions and explanations are available 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 the growth, survival, and reproduction of most organisms. All heterotrophic organisms

93 require sources of chemical energy (i.e., food), water, and various limiting nutrients (Harvey
94 and Clutton-Brock 1981; Baldwin and Bywater 1984; Reich 2001). As the abundance of
95 essential resources fluctuates, motile organisms can move to new locations or ‘patches’ to
96 meet their requirements (Charnov 1976; Brown et al. 1999), but they must also account for
97 costs of movement (Taylor et al. 1982).

98 Fig. 1 illustrates our first of two hypotheses, which is similar to that presented by
99 Harestad and Bunnel (1979). When $E(R)$ is high, we expect organisms’ ranges to be rela-
100 tively small and near the smallest amount of space required to survive (e.g., Relyea et al.
101 2000; Herfindal et al. 2005; Nilsen et al. 2005). Like Harestad and Bunnel (1979), we also
102 expect organisms’ range sizes to increase nonlinearly as $E(R)$ decreases, but we highlight
103 that organisms may adopt different behaviors at low values of $E(R)$. These behaviors include
104 maximal home range expansion (home range size is limited by vagility, habitat structure,
105 competition, and predation, e.g., Rich et al. 2012; Dawe et al. 2014; Berger-Tal and Saltz
106 2019; Tórrez-Herrera et al. 2020), migration (Samarra et al. 2017; Middleton et al. 2018;
107 Geremia et al. 2019), and nomadism (Singh et al. 2012; Polansky et al. 2015; Nandintsetseg
108 et al. 2019; Teitelbaum and Mueller 2019). It is unclear when organisms switch from range
109 residency to migration or nomadism (or vice-versa), but understanding the gradient among
110 these types of movement is necessary for quantifying the effect of resource abundance on
111 organisms’ range size and movement behavior (mammals: Teitelbaum et al. 2015; moose,
112 *Alces alces*: Singh et al. 2012; eagles, *Haliaeetus leucocephalus*: Wheat et al. 2017; Poessel
113 et al. 2022; lesser flamingos, *Phoeniconaias minor*: Pretorius et al. 2020). Still, species-level
114 changes in movement behavior are more likely to occur over evolutionary timescales than
115 over an organism’s lifespan, since larger ranges require greater vagility, which, in turn, is
116 facilitated by morphological features such as hinged joints and elongated limbs (Andersson
117 2004; Jetz et al. 2004; Samuels et al. 2013; Hirt et al. 2017).

118 Overall, the hypothesis that range size decreases with resource abundance, $E(R)$, is
119 commonly accepted and well supported, but many studies assume a linear relationship (e.g.,

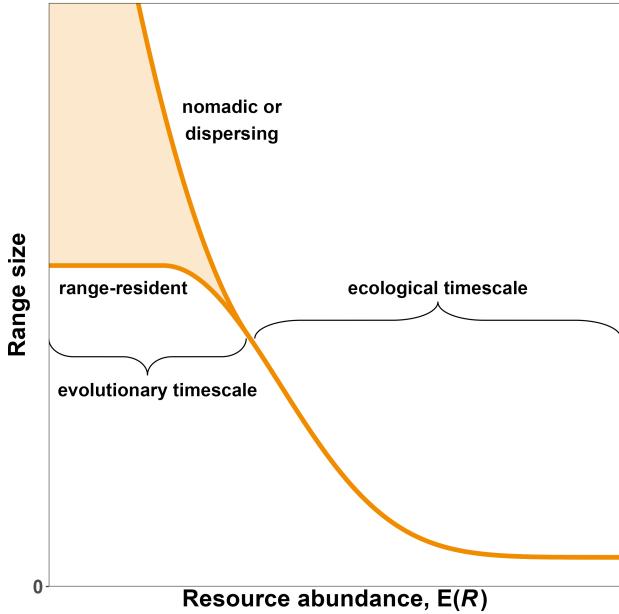


Figure 1: Hypothesized range size of an organism as a function of resource abundance, $E(R)$. We expect low values of $E(R)$ to result in a large range, since organisms are forced to explore large areas to collect the resources they require to survive, whether they be range-resident, nomadic, or migratory.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

120 Relyea et al. 2000; McClintic et al. 2014; Rizzuto et al. 2021; Bista et al. 2022; Bradsworth
 121 et al. 2022). This is problematic because, conceptually, the relationship between range
 122 size and $E(R)$ must be nonlinear, since: (1) there is an upper limit to how much space an
 123 organism is able to explore in its finite lifetime and (2) the minimum amount of space it
 124 requires to survive is necessarily greater than zero (see: Lucherini and Lovari 1996; Herfindal
 125 et al. 2005; Nilsen et al. 2005; Simcharoen et al. 2014; Watson 2020, and contrast them to
 126 the estimates based on linear models listed above). Consequently, we suggest analysts use
 127 models that account for this nonlinearity when estimating the effects of resource abundance
 128 on range size.

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

130 Assuming resource stochasticity is constant over time and space can be a useful simplification
 131 of relatively stable environments or when information on how $E(R)$ changes is limited and
 132 estimating changes in $\text{Var}(R)$ is unreasonable. However, such an assumption is likely not

133 realistic, since $\text{Var}(R)$ often differ across space and over time. Generally, strictly positive
134 quantities tend to have correlated mean and variances. For example, the number of berries
135 in a patch will be low during periods of scarcity (e.g., winter, droughts) due to both a low
136 mean (e.g., 15 berries) and a narrow range of values (e.g., 0 to 50 berries), which implies a
137 small variance. In contrast, periods of high productivity (e.g., spring green-up) will have a
138 higher mean (e.g., 500 berries) and wider range of R (e.g., 300 to 700 berries), which implies
139 a higher variance (e.g., due differences in phenology, environmental conditions, and patch
140 depletion). This relationship between a random variable's mean and variance is present
141 in many statistical distributions where values are strictly positive, such the Gamma and
142 Poisson distributions. See the section on probability distributions in Appendix A for more
143 information.

144 Recognizing changes in $\text{Var}(R)$ helps account for the residual, fine-scale variation in R
145 after accounting for trends in the large-scale average R (e.g., variations in plant phenology
146 between years after accounting for mean seasonal trends, see Levin 1992). However, when
147 both $E(R)$ and $\text{Var}(R)$ change over time (fig. A2), disentangling changes in $E(R)$ and $\text{Var}(R)$
148 is not simple (Steixner-Kumar and Gläscher 2020). Statistically, this is because the more
149 change one attributes to $\mu(t, \vec{u})$ (i.e., the wigglier it is), the smaller $\sigma^2(t, \vec{u})$ becomes. Con-
150 versely, the smoother $\mu(t, \vec{u})$ is, the larger $\sigma^2(t, \vec{u})$ becomes. Biologically, this is important
151 because an organism's perception scale determines whether it attributes a change in R to
152 a trend in $E(R)$ or as a stochastic event [i.e., due to $\text{Var}(R)$; see Levin (1992)]. An organ-
153 ism's perception of changes in R will also depend strongly on the its cognitive capacities and
154 memory (Foley et al. 2008; Fagan et al. 2013; Mueller et al. 2013; Abrahms et al. 2019;
155 Falcón-Cortés et al. 2021). Whether an organism is able to predict trends in $\sigma^2(t, \vec{u})$ or not,
156 environmental variability is thought to reduce a landscape's energetic balance (Chevin et al.
157 2010), which, in turn, decreases organisms' fitness (e.g., Berger et al. 2018) and increases
158 their range size. While this is true for both predictable and unpredictable stochasticity, ex-
159 treme and rare events are more likely to have a stronger effect due to their unpredictability

and magnitude (Logares and Nuñez 2012; Anderson et al. 2017). A few recent studies support these hypotheses (Chevin et al. 2010; Morellet et al. 2013; Nandintsetseg et al. 2019; Riotte-Lambert and Matthiopoulos 2020), but many of them are limited in geographic and taxonomic scales, so the extent to which these preliminary findings can be generalized is currently unknown. Thus, there remains a need for developing a more complete understanding of how organisms' range sizes changes with environmental stochasticity.

Similarly to $E(R)$, we hypothesize $\text{Var}(R)$ has a nonlinear effect on an organism's range size. When $\text{Var}(R)$ is low enough that R is relatively predictable, we expect organisms to be range-resident with small home ranges, and we do not expect small changes in $\text{Var}(R)$ to have a noticeable effect. As resources become increasingly unpredictable, we expect home range size to increase progressively faster (fig. 2) because: (1) as $\text{Var}(R)$ increases, the chances of finding low R increase superlinearly, (2) the added movement required to search for food increases organisms' energetic requirements, and (3) stochasticity reduces an organism's ability to specialize and reduce competition for R (Levins 1974). If resources remain highly unpredictable over long periods of time (e.g., multiple lifespans), organisms may evolve or develop new and consistent behaviors (e.g, nomadism) or adaptations (e.g., increased fat storage or food caching) to buffer themselves against times of unpredictably low R . Conversely, if changes in $\sigma^2(t, \vec{u})$ are sufficiently predictable, organisms may learn to anticipate and prepare for times of greater stochasticity by pre-emptively caching food, reducing energetic needs, migrating, or relying on alternative food sources (e.g., Van Baalen et al. 2001).

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

We have provided the case for why both $E(R)$ and $\text{Var}(R)$ should be expected to affect organisms' range size, but we presented the two parameters as independent drivers of movement. However, organisms may respond to changes in $\sigma^2(t, \vec{u})$ more when resources are scarce than when they are abundant. Consequently, an organism's movement behavior is

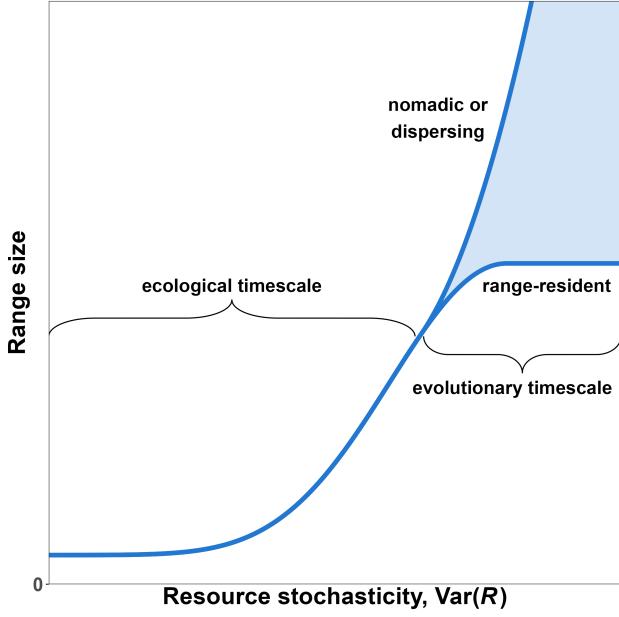


Figure 2: Hypothesized range size of an organism as a function of resource stochasticity, $\text{Var}(R)$. We expect low values of $\text{Var}(R)$ to result in small home-ranges, since organisms are able to depend on relatively predictable resources. As $\text{Var}(R)$ increases, range size should increase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

likely to be a function of not only the marginal effects of $E(R)$ and $\text{Var}(R)$ but also their interactive effects. A highly unpredictable habitat may be very inhospitable if resources are poor, but $\text{Var}(R)$ may have little effect if resources are stochastic but always abundant. Thus, we expect $\text{Var}(R)$ to have a stronger effect on range size when $E(R)$ is low, and less of an effect when $E(R)$ is high. We explore this more in the following section.

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

To support our hypotheses of how organisms' range sizes are affected by $E(R)$, $\text{Var}(R)$, and the interaction effect of $E(R)$ and $\text{Var}(R)$, we present the results from a series of quantitative simulations. To start, we used the `ctmm` package (Fleming and Calabrese 2021) for `R` (`R` Core Team 2023) to generate 200 tracks (see Appendix B for sensitivity analyses) from an Integrated Ornstein-Uhlenbeck movement model (IOU model, see Gurarie et al. 2017). The IOU model's correlated velocity produced realistic tracks with directional persistence, 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 to range-
200 resident. Consequently, each track is spatially unrestricted and can be interpreted as purely
201 exploratory or memoryless movement.

202 Each of the 200 tracks were placed on a grid with common starting point $\langle 0, 0 \rangle$ (fig. B1).
203 Each time the simulated individual moved to a new cell, it collected R resources sampled
204 from a Gamma distribution. The mean and variance of the distribution were defined by a
205 series of deterministic functions $\mu(t)$ and $\sigma^2(t)$ (orange and blue lines in fig. 3). The value
206 of t was constant within each set of 200 tracks, so the distribution R was sampled from
207 was independent of both the organism's location and its time spent moving. Tracks were
208 truncated once the organism reached satiety, and the organism was given enough time to
209 return to $\langle 0, 0 \rangle$ independently from the following track (section 2.1 of Appendix B). Finally,
210 we fit an OUF movement model (Fleming et al. 2014) to the set of tracks to calculate the
211 95% Gaussian home-range size using the formula

$$H_{95\%} = -2 \log(1 - 0.95) \pi \hat{\zeta}^2,$$

212 where $\hat{\zeta}^2$ is the positional variance estimated by the movement model.

213 We designed the simulations to estimate the effects of $E(R)$ and $\text{Var}(R)$ in simplistic
214 environments where organisms could only respond by searching for longer periods of time.
215 Consequently, we made the following assumptions:

- 216 1) Environments are homogeneous for a given t . Given t , $E(R) = \mu(t)$ and $\text{Var}(R) = \sigma^2(t)$
217 are constant over space and within each set of 200 tracks, but R is random and follows
218 a $\Gamma(\mu(t), \sigma^2(t))$ distribution.
- 219 2) There are no external pressures on the simulated organism. Resources do not deplete,
220 and there is no competition nor predator avoidance.
- 221 3) The organism has a fixed daily energetic requirement that is independent of movement
222 rates, and it cannot alter its metabolism or physiology. Additionally, the organism

223 does not have energetic reserves, so excess resources cannot be carried over to the next
224 track or t .

- 225 4) The organism is range-resident and can only respond to changes in $E(R)$ and $\text{Var}(R)$
226 by altering its home-range size. The organism does not disperse or abandon a range.
- 227 5) The organism's movement is simplistic. The organism's movement speed and direction
228 are stochastic and independent of $E(R)$ and $\text{Var}(R)$.
- 229 6) The organism has no perceptive range or memory. It is unable to detect, learn, or
230 predict where resources are abundant (high $E(R)$) or reliable (low $\text{Var}(R)$) over time
231 or space.
- 232 7) Animals only move to search for food or return to the center of their home-range after
233 reaching satiety.

234 Additional information is provided in Appendix B, including the directed acyclical graph
235 (see fig. B6 and McElreath 2016) we used to infer causal the mechanisms of changes in H
236 and estimate the direct effects of $E(R)$ and $\text{Var}(R)$ on H (contrast this with fig. C3 and the
237 empirical case study below).

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

245 The leftmost column of fig. 3 (constant $E(R)$) illustrates the effects of $\text{Var}(R)$ on H
246 while $E(R)$ remains constant. Overall, both mean H and the variance around it increase
247 with $\sigma^2(t)$ (most visible with constant $E(R)$ and linear $\text{Var}(R)$). This is because, similarly
248 to resource-poor periods, times of greater stochasticity require the organism to move over
249 larger areas for longer periods of time. This results in a greater uncertainty in how much

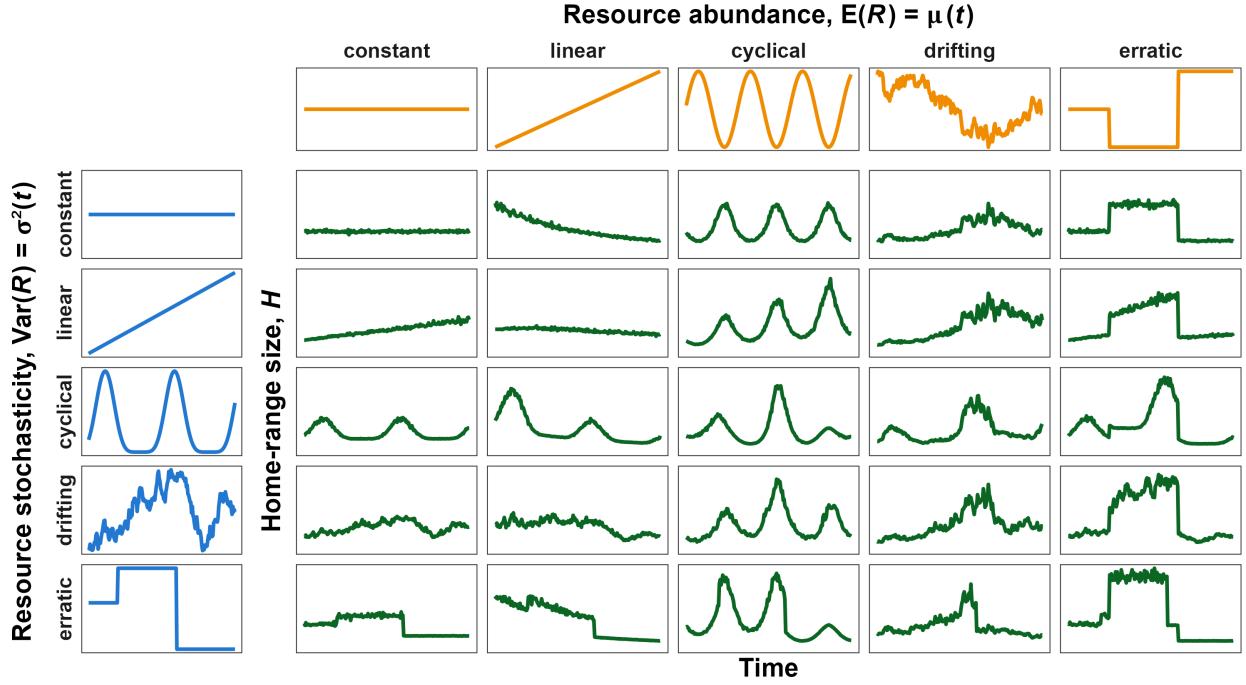


Figure 3: Simulated home-range sizes, H , of an organism living in habitats where the mean and variance in resources are constant, linearly increasing, cyclical, drifting, or erratic over time (but homogenous over space for a given t). Note how H decreases nonlinearly as $\mu(t)$ increases and increases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

time and space the organism will require to reach satiety, or indeed whether an organism living in highly stochastic environments can even reach satiety within a finite amount of time.

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

Although the temporal trends in fig. 3 are complex and the effects of $E(R)$ and $\text{Var}(R)$ can be hard to disentangle, two simple relationships emerge when H is shown as a function of either $E(R)$ or $\text{Var}(R)$, rather than time (panels A and B of fig. 4). The estimated

relationships follow the hypotheses we presented in figs. 1 and 2, although we found that the effect of $\text{Var}(R)$ at average $E(R)$ was linear with a slight sublinear saturation at high values of $\text{Var}(R)$. However, notice that the effect of $\text{Var}(R)$ on $E(H)$ depends strongly on $E(R)$ (panel C): When $E(R)$ is low, $E(H)$ is high and $\text{Var}(R)$ does not have a strong effect, but when $E(R)$ is high the effect of $\text{Var}(R)$ on $E(H)$ is exponential. Similarly, $E(H)$ decreases exponentially with $E(R)$ except when $\text{Var}(R)$ is very high.

As expected by the changes in the spread of the points in panels A and B of fig. 4, the variance in H , $\text{Var}(H)$, also depends on $E(R)$ and $\text{Var}(R)$ (fig. 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 (i.e., constant coefficient of variation, $\frac{\mu(t)}{\sigma^2(t)}$). This allowed us to show that the effect of R on $\text{Var}(H)$ is much stronger than the effect of R on $E(H)$. Consequences of these effects are explored in the discussion section.

A case study on a lowland tapir in the Brazilian Cerrado

The simulations in the section above support 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 that promote the use 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 using empirical tracking data on a lowland tapir from the Brazilian Cerrado along with empirical estimates of $E(R)$ and $\text{Var}(R)$. We measure R using Normalized Difference Vegetation Index (NDVI, see Pettorelli et al. 2011), a remote-sensed measure of landscape greenness, as a proxy for forage abundance. Appendix C contains additional information on how we modeled NDVI and the tapir's movement using continuous-time movement models (Noonan et al. 2019a; Fleming and Calabrese 2021) and

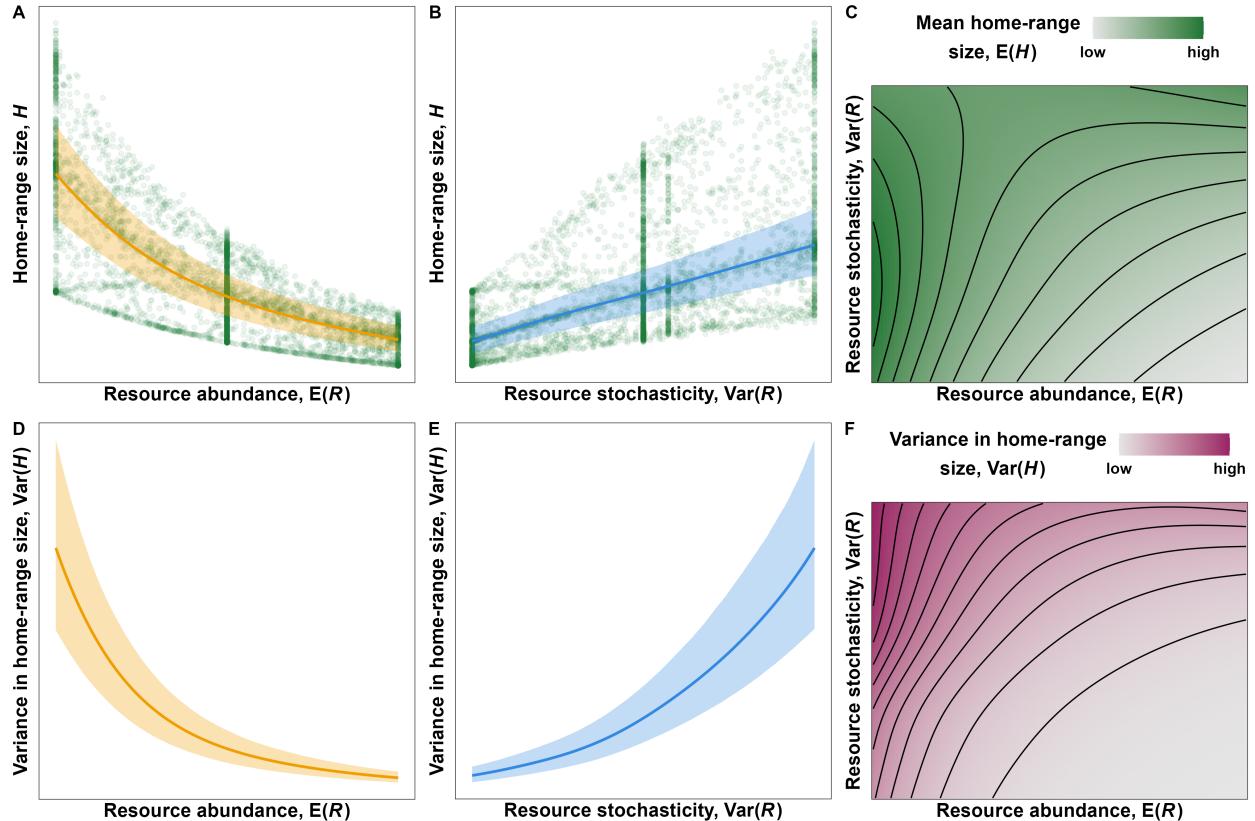


Figure 4: Effects of $E(R)$ and $\text{Var}(R)$ on the mean (A-C) and variance (D-F) in simulated home-range size with 95% Bayesian credible intervals. While the estimated marginal effect of $\text{Var}(R)$ on $E(H)$ is sublinear (panel B), the effect of $\text{Var}(R)$ is superlinear for high values of $E(R)$ (panel C). The relationships were estimated using a Generalized Additive Model for Location and Scale with a Gamma location-scale family of distributions (`mgcv::gammals`). Credible intervals were calculated using 10,000 samples from the posterior distribution while assuming multivariate Gaussian coefficients. Additional details on the model structure are provided in Appendix B.

289 autocorrelated kernel density estimation (Noonan et al. 2019b; Alston et al. 2022; Silva et
290 al. 2022).

291 Fig. 5 illustrates how a tapir in the Brazilian Cerrado adapts its 7-day home-range size to
292 spatiotemporal changes in $\mu(t, \vec{u})$ and $\sigma^2(t, \vec{u})$ (telemetry data from the individual labelled
293 as “Anna” in the dataset from Medici et al. 2022). Panels A and B show the changes in
294 seven-day average mean and variance in NDVI, respectively, experienced by the tapir during
295 the tracking period. The mean and variance in NDVI were estimated using a Generalized
296 Additive Model for Location and Scale (GAMLS, theory: Rigby and Stasinopoulos 2005;
297 Stasinopoulos and Rigby 2007; example: Gushulak et al. 2024) with a Beta family of
298 distributions (NDVI values ranged from 0.3534 to 0.9475). Panel C shows the changes in
299 the tapir’s 7-day home range over time. Note how the tapir uses more space during periods
300 of lower NDVI (e.g., August 2017) and less space during periods with high NDVI (January
301 2018). Additionally, when resources are scarce and highly unpredictable (August 2018), the
302 tapir uses up to 5 times more space than when resources are abundant and predictable (e.g.,
303 January 2018). Finally, panels D and E show the estimated (marginal) effects of $\mu(t, \vec{u})$ and
304 $\sigma^2(t, \vec{u})$ on the tapir’s 7-day home-range size. Since $\mu(t, \vec{u})$ and $\sigma^2(t, \vec{u})$ are correlated (panel
305 F) and spatiotemporally autocorrelated (panels A, B, and F), the effects of R on H should
306 be modeled carefully. To avoid over-fitting the model, we constrained the smooth effects
307 of $\mu(t, \vec{u})$ and $\sigma^2(t, \vec{u})$ and their interaction effect to a small basis size ($k = 3$). Additional
308 information is provided in appendix C. The results presented in panels D-F of fig. 5 match
309 our findings from the simulations: The tapir’s 7-day home range decreases with $\mu(t, \vec{u})$ and
310 increases with $\sigma^2(t, \vec{u})$, and the effect of $\mu(t, \vec{u})$ depends on $\sigma^2(t, \vec{u})$, and vice-versa. Alone,
311 $\mu(t, \vec{u})$ and $\sigma^2(t, \vec{u})$ cause the tapir to double her home range (panels D and E), but together
312 they result in an approximate 15-fold change in home-range size (observed range: 0.8 to 12.4
313 km²; see panel F). Additionally, note how high NDVI values (> 0.8) cause $\sigma^2(t, \vec{u})$ to have
314 little to no effect on home-range size, as indicated by the vertical contour line in panel F.

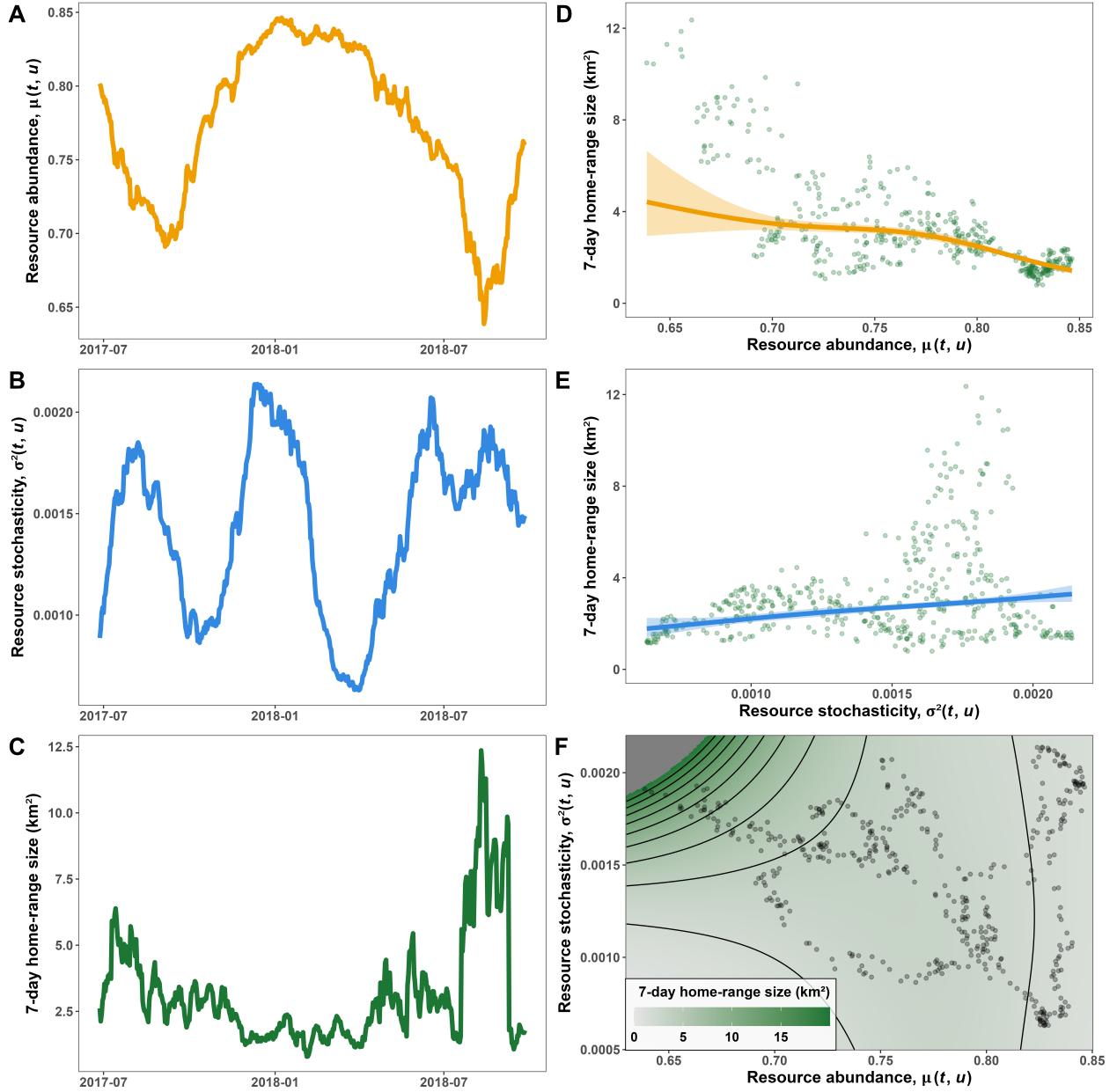


Figure 5: Effects of $\mu(t, \vec{u})$ and $\sigma^2(t, \vec{u})$ on the home-range size of a lowland tapir (*Tapirus terrestris*). (A) Trends in resource abundance over time, $\mu(t, \vec{u})$, estimated as the average mean NDVI at the locations visited by the tapir during a seven-day period. (B) Variance in resources over time, $\sigma^2(t, \vec{u})$, estimated as the average variance in NDVI at the locations visited by the tapir during a seven-day period. (C) Seven-day 95% home range estimated using Autocorrelated Kernel Density Estimation. (D, E) Estimated marginal effects of $\mu(t, \vec{u})$ and $\sigma^2(t, \vec{u})$ on home-range size. The model accounted for the marginal effects of $\mu(t, \vec{u})$ and $\sigma^2(t, \vec{u})$ and their interaction effect. (F) Estimated home-range size in response to changes in both $\mu(t, \vec{u})$ and $\sigma^2(t, \vec{u})$. Note how the effect of $\sigma^2(t, \vec{u})$ is more pronounced when $\mu(t, \vec{u})$ is low. 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).

³¹⁵ **Discussion**

³¹⁶ The amount of space organisms use is determined by a multitude of factors (Nathan et al.
³¹⁷ 2008), but the search for resources is often a main driver of animal how much and where
³¹⁸ organisms move. This paper presents two hypotheses that describe the effects of resource
³¹⁹ abundance and stochasticity on organisms' range sizes. We use quantitative simulations and
³²⁰ an empirical case study to support the hypotheses and show that, together, they provide a
³²¹ simple framework for understanding how motile organisms adapt their movement in dynamic
³²² environments.

³²³ Separately, resource abundance and stochasticity have simple but opposing effects on
³²⁴ organisms' range sizes: H decreases with $E(R)$ and increases with $\text{Var}(R)$. Together, the
³²⁵ degree to which $E(R)$ affects H depends on $\text{Var}(R)$, and vice-versa, so organisms' responses to
³²⁶ resource dynamics can be complex. The simulated and empirical results suggest qualitatively
³²⁷ similar marginal effects of $E(R)$ and $\text{Var}(R)$, but there are differences in the estimated
³²⁸ interactive effects. In the simulated data, $\text{Var}(R)$ has little effect when $E(R)$ is low and
³²⁹ a strong effect when $E(R)$ is high, while the opposite is true for the empirical data. This
³³⁰ is due to two reasons. Firstly, the shape and symmetry of bounded distributions such as
³³¹ Gamma ($R > 0$) and Beta ($0 < R < 1$) distributions depend on both $E(R)$ and $\text{Var}(R)$ (figs.
³³² A3, A4), but $\text{Var}(R)$ does not affect the shape of a Gamma distribution as much if $E(R)$ is
³³³ low (fig. B3). Secondly, and perhaps more interestingly, the simulation approach does not
³³⁴ account for real-world adaptations to $E(R)$ and $\text{Var}(R)$ such as selective space use, which
³³⁵ we account for in the empirical approach. Below we discuss the strengths and limitations of
³³⁶ each approach.

³³⁷ **Strengths and limitations of the simulation-based approach**

³³⁸ Our simulations are based on a simplistic environment with many assumptions that allowed
³³⁹ us to estimate how resource abundance and stochasticity affect organisms' home-range sizes

340 if organisms can only respond to changes by adapting the amount of time spent searching for
341 food (with no energetic cost to movement). The use of continuous-time movement models
342 coupled with few drivers of movement supported realistic data that could be explained by
343 straightforward causal models. The absence of confounding variables (e.g., predator avoid-
344 ance, territoriality, competition, landscape connectivity) or sample size limitation allowed
345 us to ensure estimates were accurate and robust (sensitivity analysis available in Appendix
346 B).

347 Deviations from the simulations offer a means of detecting when the underlying assump-
348 tions are inappropriate and how additional factors may affect organisms' responses to changes
349 in $E(R)$ and $\text{Var}(R)$. For example, energetic costs of movement are often non-negligible and
350 depend on organism size (Taylor et al. 1982), movement speed (Taylor et al. 1982), and
351 ambient temperature (Brown et al. 2004; Hou et al. 2020). In addition, an organism
352 may alter its movement behavior, physiology, and energetic needs to buffer itself against
353 changes in $E(R)$ and $\text{Var}(R)$ by using space selectively (Johnson 1980; Rickbeil et al. 2019;
354 Riotte-Lambert and Matthiopoulos 2020; Ranc et al. 2022) and adapting their behavior and
355 physiology over time (Levins 1974; Southwood 1977). Before or during periods of scarcity,
356 organisms may cache resources (Nespolo et al. 2022), enter states of dormancy (Reher et
357 al. 2018; Goldberg and Conway 2021), or even pause fetal growth (Schmidt et al. 2020).
358 However, organisms may be unable to respond to changes in $E(R)$ and $\text{Var}(R)$ optimally due
359 to various reasons, including limited perceptive range (Steixner-Kumar and Gläscher 2020),
360 lack of experience (Foley et al. 2008; Fagan et al. 2013; Polansky et al. 2015; Abrahms et
361 al. 2019; Merkle et al. 2019; Falcón-Cortés et al. 2021), and avoidance of competitors and
362 predators (Fretwell and Lucas 1969; Kacelnik et al. 1992). Failure to respond optimally may
363 thus force organisms to relocate their range to a sub-optimal location (Ciuti et al. 2012;
364 Rich et al. 2012; Burson et al. 2018; Tórrez-Herrera et al. 2020), and may exacerbate the
365 effects of $E(R)$ and $\text{Var}(R)$ on both mean range size and the variance around it.

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

367 There are two main advantages of using an empirical approach. Firstly, using real-world
368 animal movement data can produce scale-appropriate and easily interpretable estimates.
369 Secondly, empirical models directly quantify the effects of $E(R)$, $\text{Var}(R)$, and confounding
370 variables without having to design complex and time-consuming simulations. However, it is
371 not always possible to quantify confounding variables, such as competition. While there may
372 be some appropriate proxies, such as density competitors, these variables may be hard to
373 quantify, and they may not account for the confounding effects appropriately (the presence
374 of competitors may not reflect competitive pressure). This is problematic if one is interested
375 in the direct causal effect of $E(R)$ and $\text{Var}(R)$, which requires removing any non-negligible
376 confounding effects (McElreath 2016).

377 Similarly, if R is often non-measurable. Proxies of R , such as NDVI (Pettorelli et al.
378 2011), which may introduce complexities. While R and NDVI are correlated for many
379 species (e.g., Phillips et al. 2008; Merkle et al. 2016, 2019; Middleton et al. 2018; Geremia
380 et al. 2019; Seigle-Ferrand et al. 2021), the relationship between the two can be weak
381 (Gautam et al. 2019), satellite-dependent (Huang et al. 2021), and nonlinear (Fan and Liu
382 2016; Huang et al. 2021). This can introduce two sources of bias: ecosystem-level biases
383 (indicated as Z in the directed acyclical graph in fig. C3) and satellite-level confounding
384 variables (S in fig. C3).

385 Examples of ecosystem-level biases are the effects of competition, predation, habitat
386 connectivity, and movement costs, all of which can depend on habitat quality, and, conse-
387 quently, be correlated nonlinearly to R and NDVI (Jetz et al. 2004; Prox and Farine 2020).
388 Resource-rich patches can attract larger amounts of competitors (Kacelnik et al. 1992) and
389 predators (Duncan et al. 2015), which may, in turn, increase pressures from competition and
390 predation (Charnov 1976; Brown et al. 1999). However, such pressures may result in both
391 an expansion of the range (Jetz et al. 2004; Prox and Farine 2020) or a contraction, since
392 larger ranges can be harder to defend and result in higher movement costs (Grant 1993; Jetz

393 et al. 2004) and encounter rates (Martinez-Garcia et al. 2020).

394 Satellite-level confounds include information loss due to coarse spatiotemporal resolution
395 (Fan and Liu 2016; Huang et al. 2021), satellite-level error (Tian et al. 2015; Fan and Liu
396 2016; Huang et al. 2021), and other limitations of remote sensing (e.g., inability to quantify
397 specific resources or small-scale resource depletion). However, nonlinear models such as
398 Generalized Additive Models (Wood 2017) can help account for preferences for intermediate
399 values of remotely-sensed R (e.g., young grass rather than mature grasslands, see Huang et
400 al. 2021).

401 Conclusion

402 The work presented here provides a unifying framework for viewing movement as a response
403 to resource abundance and stochasticity. We provide realistic and flexible hypotheses of
404 the effects of $E(R)$ and $\text{Var}(R)$ on organisms' range sizes and movement behavior. We
405 demonstrate that organisms' range sizes decrease with resource abundance, increase with
406 resource stochasticity, and that the effects of $\text{Var}(R)$ can depend strongly on $E(R)$.

407 Recent advances in computational power have greatly increased analysts' ability to fit
408 computationally demanding models (Wood et al. 2017; Nathan et al. 2022) that allow
409 biologists to move beyond only considering changes in mean conditions. By accounting for
410 changes in stochasticity, we can start developing a more comprehensive understanding of how
411 organisms adapt to the dynamic environments organisms live in, including recent changes in
412 climate (Intergovernmental Panel On Climate Change 2023) and increases in the frequency
413 and intensity of extreme events (Logares and Nuñez 2012; Anderson et al. 2017; Grant et
414 al. 2017; Rypkema and Tuljapurkar 2021; Yao et al. 2022).

415 Conflict of interest

416 The authors declare there are no conflicts of interest.

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