

How resource abundance and resource stochasticity affect organisms' range sizes

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¹ Abstract

² **Background:** From megafauna to amoebas, the amount of space heterotrophic organisms
³ use is thought to be tightly linked to the availability of resources within their habitats,
⁴ such that organisms living in productive habitats generally require less space than those
⁵ in resource-poor habitats. This hypothesis has widespread empirical support, but existing
⁶ studies have focused primarily on responses to spatiotemporal changes in mean resources,
⁷ while responses to unpredictable changes in resources (i.e., variance in resources or resource
⁸ stochasticity) are still largely unknown. Since organisms adjust to variable environmental
⁹ conditions, failing to consider the effects of resource unpredictability can result in an in-
¹⁰ sufficient understanding of an organism's range size. **Methods:** We leverage the available
¹¹ literature to provide a unifying framework and hypothesis for the effects of resource abun-
¹² dance and stochasticity on organisms' range sizes. We then use simulated movement data
¹³ to demonstrate how the combined effects of resource abundance and stochasticity interact
¹⁴ to shape predictable patterns in range size. Finally, we test the hypothesis using real-world
¹⁵ tracking data on a lowland tapir (*Tapirus terrestris*) from the Brazilian Cerrado. **Results:**
¹⁶ Organisms' range sizes decrease nonlinearly with resource abundance and increase nonlin-
¹⁷ early with resource stochasticity, and the effects of resource stochasticity depend strongly
¹⁸ on resource abundance. Additionally, the distribution and predictability of resources can
¹⁹ exacerbate the effects of other drivers of movement, such as resource depletion, competition,
²⁰ and predation. **Conclusions:** Accounting for resource abundance and stochasticity is cru-
²¹ cial for understanding the movement behavior of free-ranging organisms. Failing to account
²² for resource stochasticity can lead to an incomplete and incorrect understanding of how and
²³ why organisms move, particularly during periods of rapid change.

²⁴ **Background**

²⁵ The amount of resources an organism is able to access is a strong determinant of its fitness.
²⁶ Resource limitations can cause individuals to experience a negative energetic balance, which
²⁷ can then result in lower fitness [1,2], altered physiology [2–5], lower chance of reproduction
²⁸ [2,6–8], and even death [9,10]. Thus, many organisms adapt their behaviors and/or physiol-
²⁹ ogy in response to changes in local resource abundance to ensure their needs are met [e.g.,
³⁰ soil amoebae *Dictyostelium spp.*: 11, plants: 12, and animals: 13].

³¹ While there are many ways that individuals can respond to resource availability, move-
³² ment represents one of the most readily available traits that motile species can adjust [14–16].
³³ The relationship between organisms' movement and resource abundance has long been of in-
³⁴ terest to biologists. In his seminal paper, Burt [17] considered the search for food as the
³⁵ primary driver for movement within an organism's home range. Three decades after, South-
³⁶ wood [18] suggested that change in resource abundance drives how organisms decide where
³⁷ to live and when to reproduce. Two years later, Harestad and Bunnel [13] proposed that the
³⁸ simplest relationship between resource abundance and an organism's home-range size is

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

³⁹ where H is the organism's home-range size, C is the organism's resource consumption rate
⁴⁰ (kcal day^{-1}), and R is the resources the organism can access ($\text{kcal day}^{-1} \text{ unit area}^{-1}$).
⁴¹ Harestad and Bunnel's model is simple to conceptualize, and it allows for testable predictions,
⁴² but few studies are structured around a set of theoretical expectations such as Harestad
⁴³ and Bunnel's hypothesis. Many researchers have since demonstrated that organisms adapt
⁴⁴ their range sizes in response to resource abundance, but results are typically reported as
⁴⁵ independent, novel findings. Perhaps more problematic is the fact that, while much work has
⁴⁶ been done on estimating organisms' responses to changes in mean resource abundance, there
⁴⁷ is little information on how organisms respond to unpredictable changes in resources [i.e.,

48 resource stochasticity, but see: 19,20–22]. Thus, there remains a need for a clear, unifying
49 hypothesis of the effects of both resource abundance and stochasticity on organisms’ range
50 sizes.

51 Here, we refer to a location’s average amount of resources as “resource abundance”, while
52 we use the phrase “resource stochasticity” to indicate the variability in resources after ac-
53 counting for changes in the mean. We argue that, on its own, a habitat’s resource abundance
54 is not sufficient to assess the habitat’s quality, nor make predictions about how much space
55 an organism might use. To see this, consider, for instance, a herbivore grazing in a grassland
56 with relatively low but constant forage availability (i.e., low mean and variance). The ani-
57 mal may require a large but constant home range size as it moves between patches in search
58 of food. If, instead, it lived in a desert with equally scarce forage but rare, sudden, and
59 strong pulses of resources (i.e., low long-term mean and high stochasticity), it may switch
60 between dispersal in search for high-resource patches and short-term range residency within
61 patches [*sensu* 15,see 23,24,25]. Previous studies suggest that resource stochasticity may
62 decrease organisms’ fitness and landscapes’ energetic balances [e.g., 26], but there is still
63 limited empirical evidence to support this hypothesis [but see: 21,27,28].

64 In this paper, we illustrate how an organism’s range size can be expected to depend on
65 both the abundance and unpredictability of resources. First, we set the theoretical back-
66 ground necessary for the successive sections by introducing key concepts and notation. Next,
67 we provide a review of the effects of resource abundance on range sizes while suggesting a
68 simple and unifying hypothesis. Afterwards, we provide a review of the effects of resource
69 stochasticity on organisms’ range sizes while suggesting a second simple and unifying hy-
70 pothesis. Subsequently, we support the hypothesis using quantitative, simulated responses
71 in range size to changes in resource abundance and stochasticity. Finally, we demonstrate
72 how this framework can be used in practice to describe the movement ecology of a lowland
73 tapir (*Tapirus terrestris*) from the Brazilian Cerrado [29].

⁷⁴ **Resources as a random variable**

⁷⁵ Resources (e.g., food, water, shelter, heat) are often unpredictable (and difficult to quantify),
⁷⁶ since they depend on various factors which cannot be accounted for easily, including climate
⁷⁷ [7,30,31], weather [31,32], competitive pressure [33,34], and differences in energetics at among
⁷⁸ individuals [7] and species [35]. Thus, it is possible to treat the amount of resources R at a
⁷⁹ given point in time (t) and space (location vector \vec{u}) as a random variable, denoted as $R(t, \vec{u})$.
⁸⁰ Treating resources as a random variable allows us to leverage techniques from probability
⁸¹ theory and statistics, such as the expectation of a random variable (i.e., its mean) and its
⁸² variance around the mean. We indicate the expected value and variance of random variable
⁸³ R using $E(R)$ and $\text{Var}(R)$, respectively, and we use $\mu(t, \vec{u})$ and $\sigma^2(t, \vec{u})$ to indicate them
⁸⁴ as functions of time (t) and space (\vec{u}). Appendix A defines and expands on the concepts
⁸⁵ of probability distributions, expected value, variance, and provides examples of them for
⁸⁶ Gamma and Beta distributions.

⁸⁷ **Effects of resource abundance, $E(R)$**

⁸⁸ While organisms' needs vary greatly between taxonomic groups, some needs are essential
⁸⁹ for the growth, survival, and reproduction of most organisms. All heterotrophic organisms
⁹⁰ require sources of chemical energy (i.e., food), water, and various limiting nutrients [36–38].
⁹¹ As the abundance of essential resources fluctuates, motile organisms can move to new loca-
⁹² tions or 'patches' to meet their requirements [15,39], but movement also increases energetic
⁹³ needs [40].

⁹⁴ When $E(R)$ is high, we expect organisms' ranges to be relatively small and near the
⁹⁵ smallest amount of space required to survive [see fig. 1A as well as: 27,28,41]. Like Harestad
⁹⁶ and Bunnel [13], we also expect organisms' range sizes to increase nonlinearly as $E(R)$
⁹⁷ decreases, but we highlight that organisms may adopt different behaviors at low values of
⁹⁸ $E(R)$. These behaviors include maximal home range expansion [home range size is limited by

vagility, habitat structure, competition, and predation, e.g., 33,34,42,43], migration [44–46], and nomadism [23,25,47,48]. It is unclear when organisms switch from range residency to migration or nomadism (or vice-versa), but understanding the gradient among these types of movement is necessary for quantifying the effect of resource abundance on organisms' range size and movement behavior [mammals: 49, moose, *Alces alces*: 23, eagles, *Haliaeetus leucocephalus*: 24,50, lesser flamingos, *Phoeniconaias minor*: 51].

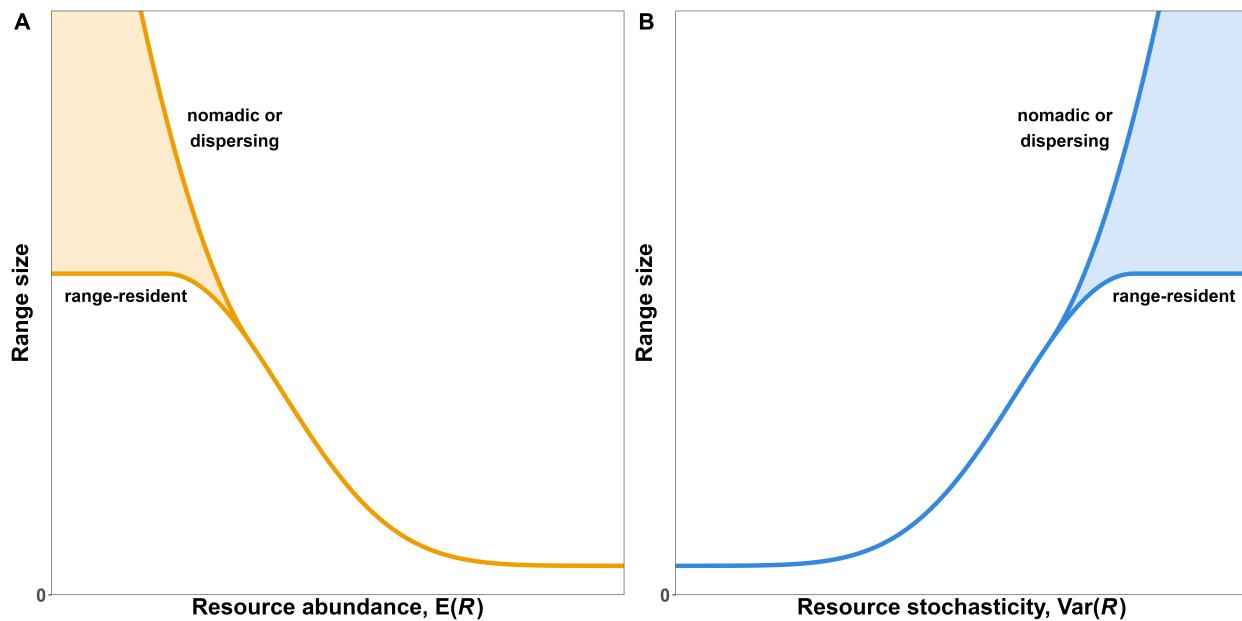


Figure 1: Hypothesized range size of an organism as a function of (A) resource abundance and (B) resource stochasticity. We expect low values of $E(R)$ and large values of $\text{Var}(R)$ to result in a large range, since organisms are forced to explore large areas to collect the resources they require to survive, whether they be range-resident, nomadic, or migratory. As $E(R)$ increases or $\text{Var}(R)$ decreases, range size should decrease nonlinearly until it reaches the minimum amount of space required by the organism to survive.

Note that the relationship between range size and both $E(R)$ and $\text{Var}(R)$ cannot be of the form $H = \beta_0 + \beta_1 E(R) + \beta_2 \text{Var}(R)$ because it would require range size to be negative for high values of $E(R)$ or low values of $\text{Var}(R)$.

Overall, the hypothesis that range size decreases with resource abundance, $E(R)$, is commonly accepted and well supported, but many studies assume a linear relationship [e.g., 21,41,52–54]. This is problematic because, conceptually, the relationship between range size and $E(R)$ must be nonlinear, since: (1) there is an upper limit to how much space an organism is able to explore in its finite lifetime and (2) the minimum amount of space it requires to survive is necessarily greater than zero [see 27,28,55,56,57, and contrast them to

the earlier references that assume a linear relationship between H and R]. Consequently, we suggest analysts use models that account for this nonlinearity when estimating the effects of resource abundance on range size. While the relationship may be approximately linear for some range of $E(R)$, this assumption often does not hold for low or high values of $E(R)$ [e.g., 52]. Additionally, identifying inflection points in nonlinear relationships can help understand the pressures and limitations of increasing range size.

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

Assuming resource stochasticity is constant over time and space can be a useful simplification of relatively stable environments or when information on how $E(R)$ changes is limited and estimating changes in $\text{Var}(R)$ is unreasonable. However, such an assumption is likely not realistic, since $\text{Var}(R)$ often differ across space and over time. Generally, bounded quantities have correlated means and variances, as in the case of random variables that are strictly positive (e.g., Gamma and Poisson) or fully bounded (e.g., Beta). For example, prey abundance in a given area over time may approximately follow a Poisson distribution, which implies that the mean and variance will be approximately equal. When prey are scarce, the variance will also be low, and when prey are abundant the variance will also be high. This occurs because the behavior, fitness, and predator-prey dynamics of many prey are more stochastic than those of few prey [58]. Similarly, in the case of fully bounded random variables, the variance is generally lowest when the mean is near either boundary. For example, successful predation events are predictably scarce if the probability of capture is near 0, predictably common if the probability is near 1, and most stochastic if the probability is near 0.5 [i.e., as far as possible from both 0 and 1; see [59]]. See Appendix A for more information.

Recognizing changes in $\text{Var}(R)$ helps account for the residual, fine-scale variation in R after accounting for trends in the large-scale average R [e.g., variations in plant phenology between years after accounting for mean seasonal trends, see 60]. However, when both $E(R)$ and $\text{Var}(R)$ change over time (fig. A2), disentangling changes in $E(R)$ and $\text{Var}(R)$ is

¹³⁷ not simple [61]. Statistically, this confound occurs because the more change one attributes
¹³⁸ to $\mu(t, \vec{u})$ (i.e., the wigglier it is), the smaller $\sigma^2(t, \vec{u})$ becomes. Conversely, the smoother
¹³⁹ $\mu(t, \vec{u})$ is, the larger $\sigma^2(t, \vec{u})$ becomes. Biologically, it is important because an organism's
¹⁴⁰ perception scale determines whether it attributes a change in R to a trend in $E(R)$ or as
¹⁴¹ a stochastic event [i.e., due to $\text{Var}(R)$; see [60]]. An organism's perception of changes in
¹⁴² R will also depend strongly on the its cognitive capacities and memory [9,62–65]. Whether
¹⁴³ an organism is able to predict trends in $\sigma^2(t, \vec{u})$ or not, environmental variability is thought
¹⁴⁴ to reduce a landscape's energetic balance [26], which, in turn, decreases organisms' fitness
¹⁴⁵ [e.g., 10] and increases their range size. While this behavioral response occurs with both
¹⁴⁶ predictable and unpredictable stochasticity, extreme and rare events are more likely to have
¹⁴⁷ a stronger effect due to their unpredictability and magnitude [66,67]. A few recent studies
¹⁴⁸ support these hypotheses [22,26,31,48,68], but many of them are limited in geographic and
¹⁴⁹ taxonomic scales or fail to account for nonlinear relationships, so the extent to which these
¹⁵⁰ preliminary findings can be generalized is currently unknown. Thus, there remains a need
¹⁵¹ for developing a more complete understanding of how organisms' range sizes changes with
¹⁵² environmental stochasticity.

¹⁵³ Similarly to $E(R)$, we hypothesize $\text{Var}(R)$ has a nonlinear effect on an organism's range
¹⁵⁴ size. When $\text{Var}(R)$ is low enough that R is relatively predictable, we expect organisms to
¹⁵⁵ be range-resident with small home ranges, and we do not expect small changes in $\text{Var}(R)$ to
¹⁵⁶ have a noticeable effect. As resources become increasingly unpredictable, we expect home
¹⁵⁷ range size to increase progressively faster (fig. 1B) because: (1) as $\text{Var}(R)$ increases, the
¹⁵⁸ chances of finding low R increase superlinearly, (2) the added movement required to search
¹⁵⁹ for food increases organisms' energetic requirements, and (3) stochasticity reduces an or-
¹⁶⁰ ganism's ability to specialize and reduce competition for R [69]. If resources remain highly
¹⁶¹ unpredictable over long periods of time (e.g., multiple lifespans), organisms may evolve or
¹⁶² develop new and consistent behaviors (e.g, nomadism) or adaptations (e.g., increased fat
¹⁶³ storage or food caching) to buffer themselves against times of unpredictably low R . Con-

164 versely, if changes in $\sigma^2(t, \vec{u})$ are sufficiently predictable, organisms may learn to anticipate
165 and prepare for times of greater stochasticity by pre-emptively caching food, reducing
166 energetic needs, migrating, or relying on alternative food sources [e.g., 70].

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

168 We have provided the case for why both $E(R)$ and $\text{Var}(R)$ should be expected to affect
169 organisms' range size, but we presented the two parameters as independent drivers of move-
170 ment. However, organisms may respond to changes in $\sigma^2(t, \vec{u})$ more when resources are
171 scarce than when they are abundant. Consequently, an organism's movement behavior is
172 likely to be a function of not only the marginal effects of $E(R)$ and $\text{Var}(R)$ but also their
173 interactive effects. A highly unpredictable habitat may be very inhospitable if resources
174 are poor, but $\text{Var}(R)$ may have little effect if resources are stochastic but always abundant.
175 Thus, we expect $\text{Var}(R)$ to have a stronger effect on range size when $E(R)$ is low, and less of
176 an effect when $E(R)$ is high. We explore this interaction effect more in the following section.

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

178 To evaluate our hypothesis of how organisms' range sizes are affected by $E(R)$, $\text{Var}(R)$, and
179 the interaction effect of $E(R)$ and $\text{Var}(R)$, we present the results from a series of quantitative
180 simulations. To start, we used the `ctmm` package [71] for R [72] to generate 200 tracks (see Ap-
181 pendix B for sensitivity analyses) from an Integrated Ornstein-Uhlenbeck movement model
182 [IOU model, see 73]. The IOU model's correlated velocity produced tracks with directional
183 persistence, but, unlike Ornstein-Uhlenbeck (OU) and Ornstein-Uhlenbeck Foraging (OUF)
184 models, IOU models do not produce spatially stationary movement, so the organism is not
185 range-resident. Consequently, each track is spatially unrestricted and can be interpreted as
186 purely exploratory or memoryless movement.

187 Each of the 200 tracks were placed on a grid with common starting point $\langle 0, 0 \rangle$ (fig. B1).
188 Each time the simulated individual moved to a new cell, it collected R resources sampled

189 from a Gamma distribution. The mean and variance of the distribution were defined by a
 190 series of deterministic functions $\mu(t)$ and $\sigma^2(t)$ (orange and blue lines in fig. 3). The value
 191 of t was constant within each set of 200 tracks, so the distribution R was sampled from
 192 was independent of both the organism's location and its time spent moving. Tracks were
 193 truncated once the organism reached satiety, and the organism was given enough time to
 194 return to $\langle 0, 0 \rangle$ independently from the following track (section 2.1 of Appendix B). Finally,
 195 we fit an OUF movement model [74] to the set of tracks to calculate the 95% Gaussian
 196 home-range size using the formula

$$\hat{H}_{95\%} = -2 \log(1 - 0.95) \pi \hat{\varsigma}^2,$$

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

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

- 201 1) Environments are homogeneous for a given t . Given t , $E(R) = \mu(t)$ and $\text{Var}(R) = \sigma^2(t)$
 202 are constant over space and within each set of 200 tracks, but R is random and follows
 203 a $\text{Gamma}(\mu(t), \sigma^2(t))$ distribution.
- 204 2) There are no external pressures on the simulated organism. Resources do not deplete,
 205 and there is no competition nor predator avoidance.
- 206 3) The organism has a fixed daily energetic requirement that is independent of movement
 207 rates, and it cannot alter its metabolism or physiology. Additionally, the organism
 208 does not have energetic reserves, so excess resources cannot be carried over to the next
 209 track or t .
- 210 4) The organism is range-resident and can only respond to changes in $E(R)$ and $\text{Var}(R)$
 211 by altering its home-range size. The organism does not disperse or abandon a range.
- 212 5) The organism's movement is simplistic. The organism's movement speed and direction

213 are stochastic and independent of $E(R)$ and $\text{Var}(R)$.

- 214 6) The organism has no perceptive range or memory. It is unable to detect, learn, or
215 predict where resources are abundant (high $E(R)$) or reliable (low $\text{Var}(R)$) over time
216 or space.
- 217 7) Animals only move to search for food or return to the center of their home-range after
218 reaching satiety.

219 Based on the assumptions above, we constructed the following causal model for the
220 simulated effects of $E(R)$ and $\text{Var}(R)$ on H [see fig. 2 and 75]: $E(R)$ and $\text{Var}(R)$ were
221 determined independently of each other, but they jointly determined the distribution of R ,
222 which, in turn, determined the distribution of H . Additional information is provided in
223 Appendix B.

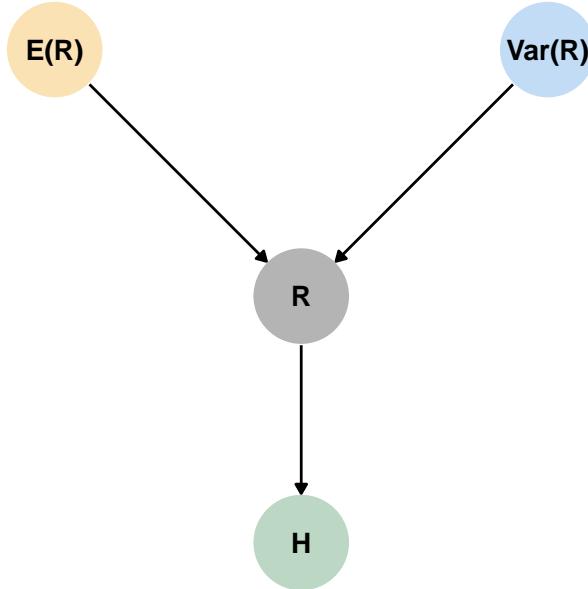


Figure 2: Directed acyclical graph assumed for inferring the causal effects of $E(R)$ and $\text{Var}(R)$ on the distributions of R and H in the simulations.

224 Fig. 3 shows how simulated home-range size, H , responded to changes in $\mu(t)$ and $\sigma^2(t)$
225 in scenarios where both functions can remain constant, increase linearly, oscillate cyclically,
226 drift stochastically, or change erratically. The top row (constant $\text{Var}(R)$) shows how H varies
227 for different trends in $\mu(t)$ while $\text{Var}(R)$ remains constant (like in fig. A1). As $E(R)$ increases

228 at a constant slope (linear $\mu(t)$), H decreases nonlinearly, with larger changes when $E(R)$
 229 is low, until it approaches the minimum size required by the organism. Also note how the
 230 noise in the green lines also decreases as $E(R)$ increases.

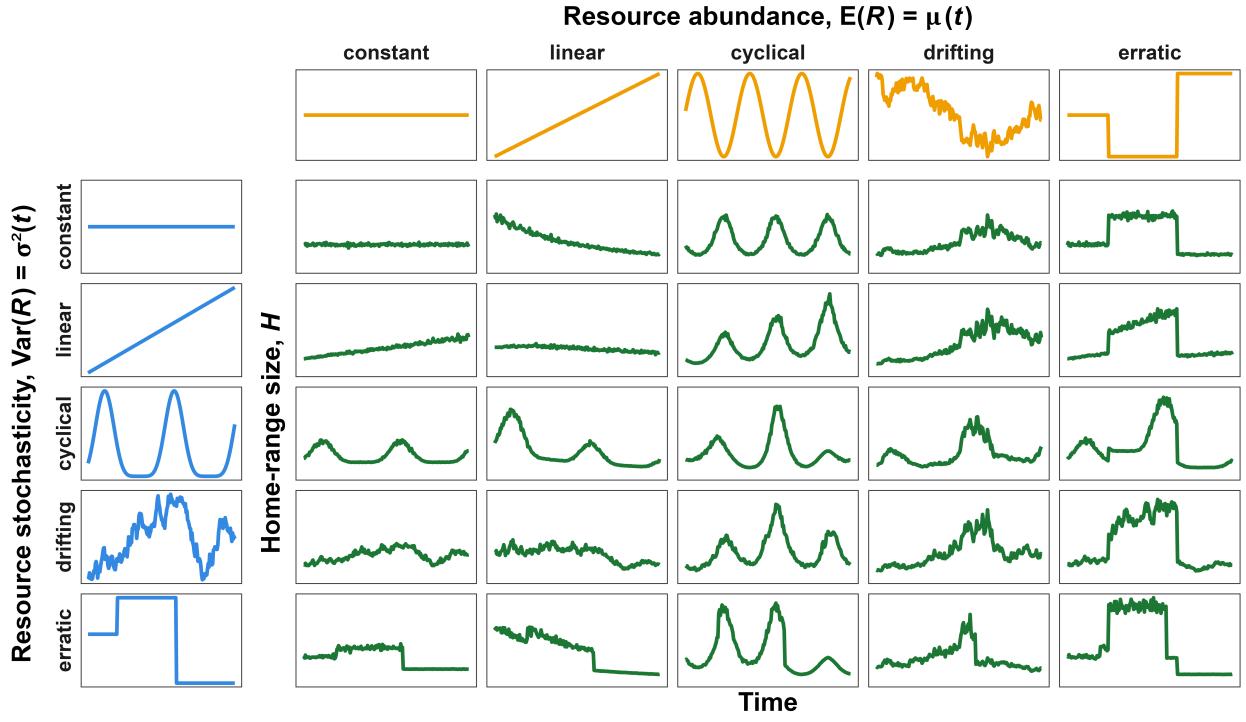


Figure 3: Simulated home-range sizes, H , of an organism living in habitats where the mean and variance in resources are constant, linearly increasing, cyclical, drifting, or erratic over time (but homogeneous over space for a given t). Note how H decreases nonlinearly as $\mu(t)$ increases and increases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

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

238 The remaining panels in fig. 3 illustrate how $E(R)$ and $\text{Var}(R)$ jointly affect H and
 239 how unintuitive the effects can be. Since $E(R)$ and $\text{Var}(R)$ have opposite effects on H ,
 240 disentangling the effects can be particularly difficult when both parameters change in a

241 correlated manner (e.g., linear $E(R)$ and $\text{Var}(R)$). When both $E(R)$ and $\text{Var}(R)$ increase
242 linearly, H initially increases since the effect of $\text{Var}(R)$ is stronger, but then decreases as the
243 effect of $E(R)$ begins to dominate. Difficulties in disentangling the two effects are explored
244 in greater depth in the case study in the following section.

245 Although the temporal trends in fig. 3 are complex and the effects of $E(R)$ and $\text{Var}(R)$
246 can be hard to disentangle, two simple relationships emerge when H is shown as a function of
247 either $E(R)$ or $\text{Var}(R)$, rather than time: H decreases nonlinearly with $E(R)$ and increases
248 with $\text{Var}(R)$ (panels A and B of fig. 4). The estimated relationships thus follow the hypothesis
249 we presented in fig. 1, although we found that the effect of $\text{Var}(R)$ at average $E(R)$ was linear
250 with a slight sublinear saturation at high values of $\text{Var}(R)$. However, notice that the effect of
251 $\text{Var}(R)$ on $E(H)$ depends strongly on $E(R)$ (panel C): When $E(R)$ is low, $E(H)$ is high and
252 $\text{Var}(R)$ does not have a strong effect, but when $E(R)$ is high the effect of $\text{Var}(R)$ on $E(H)$
253 is exponential. Similarly, $E(H)$ decreases exponentially with $E(R)$ except when $\text{Var}(R)$ is
254 very high.

255 As expected by the changes in the spread of the points in panels A and B of fig. 4, the
256 variance in H , $\text{Var}(H)$, also depends on $E(R)$ and $\text{Var}(R)$ (fig. 4D-F). Since we modeled
257 H using a Gamma family of distributions, we expected $\text{Var}(H)$ to increase with $E(H)$, but
258 the location-scale model removes the assumption of a constant mean-variance relationship
259 (i.e., constant coefficient of variation, $\frac{\mu(t)}{\sigma^2(t)}$). This allowed us to show that the effect of R on
260 $\text{Var}(H)$ is much stronger than the effect of R on $E(H)$. Consequences of these effects are
261 explored in the discussion section.

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

263 The simulations in the section above support the hypothesis we presented in the background
264 section, but they are based on assumptions that are often not met in real natural environ-
265 ments. Organisms live in spatiotemporally heterogeneous and dynamic environments that
266 promote the use of perceptual ranges, navigation, and memory. Together, these abilities

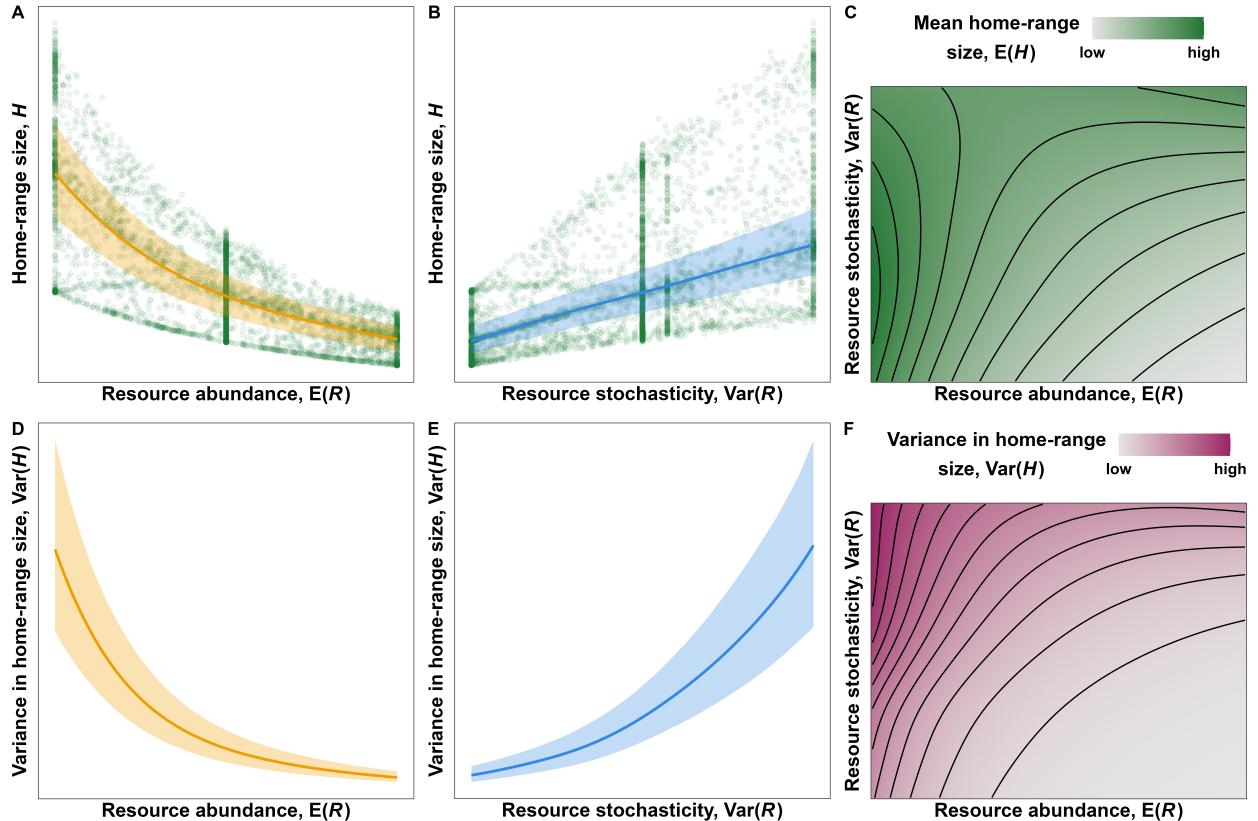


Figure 4: Effects of $E(R)$ and $\text{Var}(R)$ on the mean (A-C) and variance (D-F) in simulated home-range size with 95% Bayesian credible intervals. While the estimated marginal effect of $\text{Var}(R)$ on $E(H)$ is sublinear (panel B), the effect of $\text{Var}(R)$ is superlinear for high values 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.

267 result in selective space use that depends on resource availability [14] and resource depletion
268 [15].

269 In this section, we test the hypothesis using empirical tracking data on a lowland tapir
270 from the Brazilian Cerrado along with empirical estimates of $E(R)$ and $\text{Var}(R)$. We measure
271 R using Normalized Difference Vegetation Index [NDVI, see 76], a remote-sensed measure
272 of landscape greenness, as a proxy for forage abundance. Appendix C contains additional
273 information on how we modeled NDVI and the tapir’s movement using continuous-time
274 movement models [71,77] and autocorrelated kernel density estimation [78–80].

275 Fig. 5 illustrates how a tapir in the Brazilian Cerrado adapted its 7-day home-range
276 size to spatiotemporal changes in estimated $\mu(t, \vec{u})$ and $\sigma^2(t, \vec{u})$ (telemetry data from the
277 individual labelled as “Anna” in the dataset from [29]). Panels A and B show the changes in
278 seven-day average mean and variance in NDVI, respectively, experienced by the tapir during
279 the tracking period. The mean and variance in NDVI were estimated using a Generalized
280 Additive Model for Location and Scale [GAMLS, 81] with a Beta family of distributions
281 (NDVI values ranged from 0.3534 to 0.9475). Panel C shows the changes in the tapir’s 7-day
282 home range over time. All 457 of the 7-day windows had a minimum effective sample size
283 of 7 range crossings [range: 7.7 – 69.6, see 82], and 92% had resolvable (i.e., non-NA) home
284 range crossing times, all of which were below 17 hours. Note how the tapir uses more space
285 during periods of lower NDVI (e.g., August 2017) and less space during periods with high
286 NDVI (January 2018). Additionally, when resources are scarce and highly unpredictable
287 (August 2018), the tapir uses up to 5 times more space than when resources are abundant
288 and predictable (e.g., January 2018). Finally, panels D and E show the estimated (marginal)
289 effects of $\hat{\mu}(t, \vec{u})$ and $\hat{\sigma}^2(t, \vec{u})$ on the tapir’s 7-day home-range size. Since $\hat{\mu}(t, \vec{u})$ and $\hat{\sigma}^2(t, \vec{u})$
290 are correlated (panel F) and spatiotemporally autocorrelated (panels A, B, and F), the effects
291 of R on H should be modeled carefully. To avoid over-fitting the model, we constrained
292 the smooth effects of $\hat{\mu}(t, \vec{u})$ and $\hat{\sigma}^2(t, \vec{u})$ and their interaction effect to a small basis size
293 ($k = 3$). Additional information is provided in appendix C. The results presented in panels

²⁹⁴ D-F of fig. 5 match our findings from the simulations (fig. 4A-C): The tapir's 7-day home
²⁹⁵ range decreases with $\hat{\mu}(t, \vec{u})$ and increases with $\hat{\sigma}^2(t, \vec{u})$, and the effect of $\hat{\mu}(t, \vec{u})$ depends on
²⁹⁶ $\hat{\sigma}^2(t, \vec{u})$, and vice-versa. Alone, $\hat{\mu}(t, \vec{u})$ and $\hat{\sigma}^2(t, \vec{u})$ cause the tapir to double her home range
²⁹⁷ (panels D and E), but together they result in an approximate 15-fold change in home-range
²⁹⁸ size (observed range: 0.8 to 12.4 km²; see panel F). Additionally, note how high NDVI values
²⁹⁹ ($\hat{\mu}(t, \vec{u}) > 0.8$) cause $\hat{\sigma}^2(t, \vec{u})$ to have little to no effect on home-range size, as indicated by the
³⁰⁰ vertical contour line in panel F. Similar conclusions can be drawn for the animal's diffusion
³⁰¹ (i.e., area covered per unit time), which is a more appropriate measure of space use when
³⁰² animals are not range resident [82].

³⁰³ Quantifying the direct effects of $E(R)$ and $\text{Var}(R)$ on H using empirical data is more
³⁰⁴ complex than with simulated data, and it requires a different causal framework, particularly
³⁰⁵ in the case of observational studies (as opposed to experimentally-controlled studies; see
³⁰⁶ fig. 6). Unlike with the simulations, $E(R)$ and $\text{Var}(R)$ are not controlled variables and instead
³⁰⁷ depend on the distribution of R , which depends on a variety of other factors (that we exclude
³⁰⁸ from the figure for simplicity). Both $E(R)$ and $\text{Var}(R)$ then impact H as well as habitat-level
³⁰⁹ variables (e.g., competition, predation, etc.; indicated as Z) that also affect H . Additionally,
³¹⁰ estimating R via a proxy (NDVI) adds satellite-level noise and confounds [e.g., saturation,
³¹¹ cloud cover, spatiotemporal averaging – indicated as S , see 83,84,85]. However, $E(R)$ and
³¹² $\text{Var}(R)$ can be correlated to $E(\text{NDVI})$ and $\text{Var}(\text{NDVI})$, respectively, provided that analysts
³¹³ use models that are sufficiently smooth and flexible at the relevant spatiotemporal scale [86].
³¹⁴ We discuss this in further detail in the section below on the strengths and limitations of the
³¹⁵ empirical approach.

³¹⁶ Discussion

³¹⁷ The amount of space organisms use is determined by a multitude of factors [16], but the
³¹⁸ search for resources is often a main driver of how much and where organisms move. This
³¹⁹ paper builds on earlier theoretical work [13,e.g., 18,19] and presents a unifying hypothesis

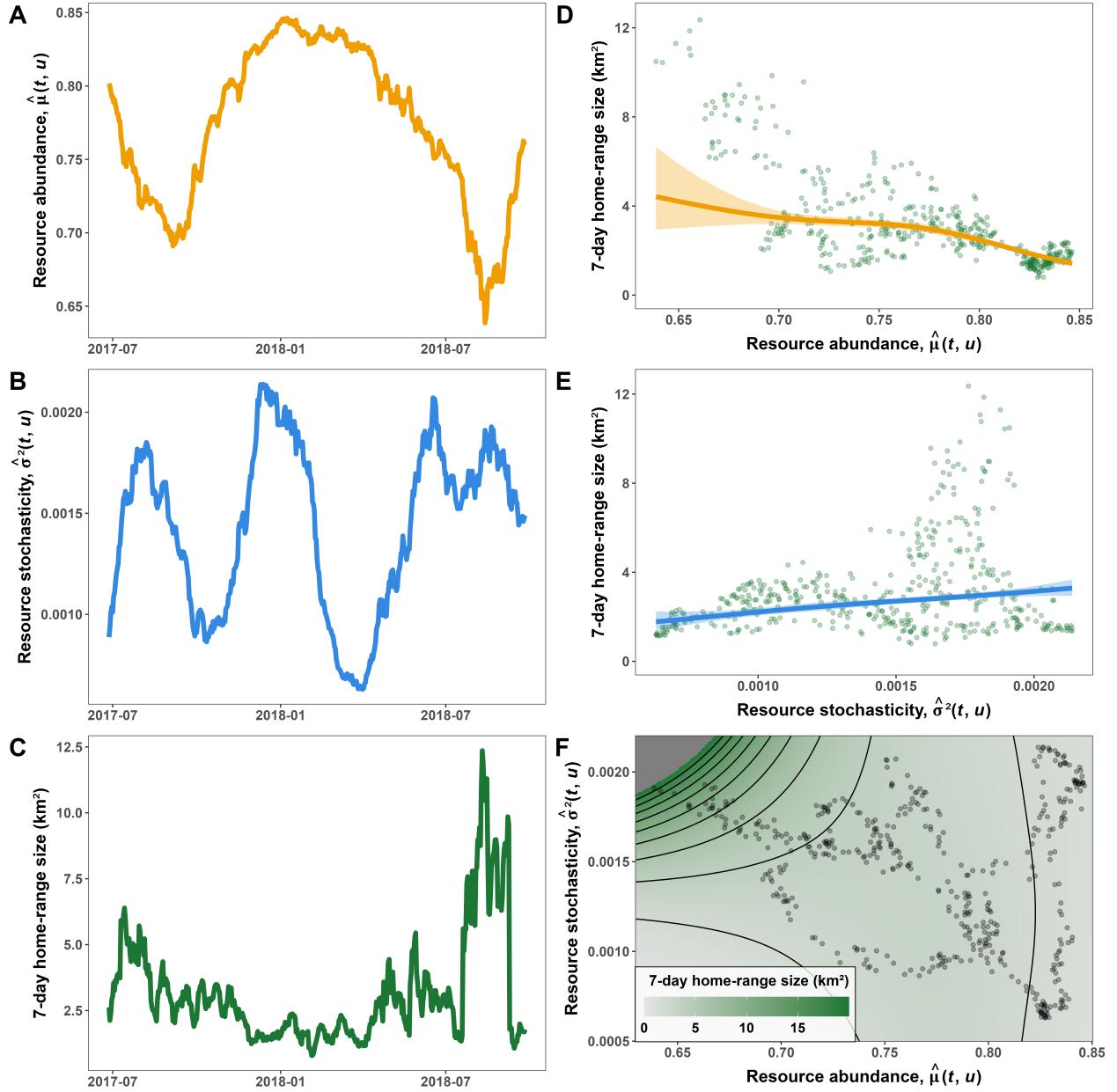


Figure 5: Effects of estimated $\mu(t, \bar{u})$ and $\sigma^2(t, \bar{u})$ on the home-range size of a lowland tapir (*Tapirus terrestris*). (A) Trends in resource abundance over time, $\hat{\mu}(t, \bar{u})$, estimated as the average mean NDVI at the locations visited by the tapir during a seven-day period. (B) Variance in resources over time, $\hat{\sigma}^2(t, \bar{u})$, 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 $\hat{\mu}(t, \bar{u})$ and $\hat{\sigma}^2(t, \bar{u})$ on home-range size. The model accounted for the marginal effects of $\hat{\mu}(t, \bar{u})$, $\hat{\sigma}^2(t, \bar{u})$, and their interaction effect. (F) Estimated home-range size in response to changes in both $\hat{\mu}(t, \bar{u})$ and $\hat{\sigma}^2(t, \bar{u})$. Note how the effect of $\hat{\sigma}^2(t, \bar{u})$ is more pronounced when $\hat{\mu}(t, \bar{u})$ 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.* [29].

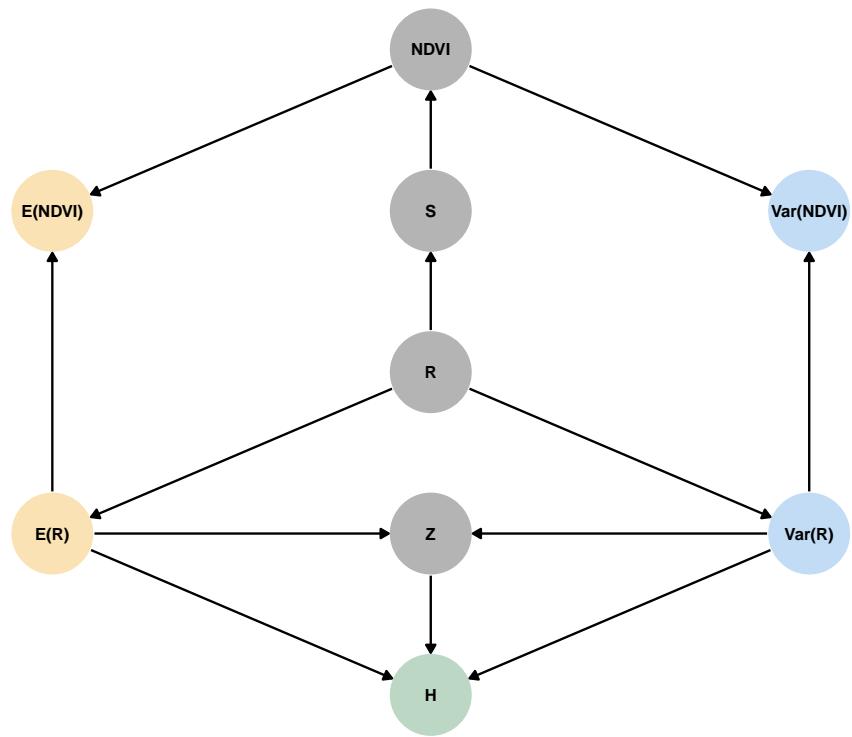


Figure 6: Directed Acyclical Graph assumed for inferring the causal effects of $E(R)$ and $Var(R)$ on H , where NDVI was used as a proxy for R . Z and S indicate confounds that result from habitat-level variables (e.g., competition, predation, etc.) and satellite-level variables (e.g., noise, cloud cover).

that describes the effects of resource abundance and stochasticity on organisms' range sizes. We use quantitative simulations and an empirical case study to support the hypothesis and show that it provides a simple framework for understanding how motile organisms adapt their movement in dynamic environments. Separately, resource abundance and stochasticity have simple but opposing effects on organisms' range sizes: H decreases with $E(R)$ and increases with $\text{Var}(R)$. Together, the degree to which $E(R)$ affects H depends on $\text{Var}(R)$, and vice-versa, so organisms' responses to resource dynamics can be complex. The simulated and empirical results suggest qualitatively similar marginal effects of $E(R)$ and $\text{Var}(R)$, but there are differences in the estimated interactive effects. In the simulated data, $\text{Var}(R)$ has little effect when $E(R)$ is low and a strong effect when $E(R)$ is high, while the opposite is true for the empirical data. This difference is due to two reasons. Firstly, the shape and symmetry of bounded distributions such as Gamma ($R > 0$) and Beta ($0 < R < 1$) distributions depend on both $E(R)$ and $\text{Var}(R)$ (figs. A3, A4), but $\text{Var}(R)$ does not affect the shape of a Gamma distribution as much if $E(R)$ is low (fig. B3). Secondly, and perhaps more interestingly, the simulation approach does not account for real-world adaptations to $E(R)$ and $\text{Var}(R)$ such as selective space use, which are included (but not explicitly accounted for) in the empirical approach. Below we discuss the strengths and limitations of each approach.

Strengths and limitations of the simulation-based approach

Our simulations are based on a simplistic environment with many assumptions that allowed us to estimate how resource abundance and stochasticity affect organisms' home-range sizes if organisms can only respond to changes by adapting the amount of time spent searching for food (with no energetic cost to movement). The use of continuous-time movement models coupled with few drivers of movement supported realistic data that could be explained by straightforward causal models. The absence of confounding variables (e.g., predator avoidance, territoriality, competition, landscape connectivity; see Figure 2) or sample size limitation allowed us to ensure estimates were accurate and robust (sensitivity analysis available

³⁴⁶ in Appendix B).

³⁴⁷ Deviations from the simulations offer a means of detecting when the underlying assumptions
³⁴⁸ 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 [40], movement speed [40], and ambient temperature [1,87]. In addition,
³⁵¹ an organism may alter its movement behavior, physiology, and energetic needs to buffer
³⁵² itself against changes in $E(R)$ and $\text{Var}(R)$ by using space selectively [68,88–90] and adapting
³⁵³ their behavior and physiology over time [18,69]. Before or during periods of scarcity, organisms
³⁵⁴ may cache resources [91], build up fat reserves [45], enter states of dormancy [92–94],
³⁵⁵ or even pause fetal growth [7]. However, organisms may be unable to respond to changes
³⁵⁶ in $E(R)$ and $\text{Var}(R)$ optimally due to various reasons, including limited perceptive range
³⁵⁷ [61], lack of experience [9,47,63–65,95], avoidance of competitors and predators [14,96], or a
³⁵⁸ physiology that is not amenable to things like hibernation or fat storage. Thus, organisms
³⁵⁹ may relocate their range to a sub-optimal location [33,34,97,98], which may exacerbate the
³⁶⁰ effects of $E(R)$ and $\text{Var}(R)$ on both mean range size and the variance around it.

³⁶¹ Strengths and limitations of the empirical approach

³⁶² There are two main advantages of taking an empirical approach. Firstly, modeling real-world
³⁶³ animal movement data can produce scale-appropriate and easily interpretable estimates.
³⁶⁴ Secondly, empirical data contain information on the effects of $E(R)$, $\text{Var}(R)$, and confounding
³⁶⁵ variables without having to design complex and time-consuming simulations. However, it
³⁶⁶ is not always possible to quantify confounding variables. For example, while there may be
³⁶⁷ some appropriate proxies of competition, such as density of competitors, these variables may
³⁶⁸ be hard to quantify, and they may not account for the confounding effects appropriately
³⁶⁹ (i.e., the presence of competitors may not reflect competitive pressure). This is problematic
³⁷⁰ if one is interested in estimating the direct causal effect of $E(R)$ and $\text{Var}(R)$, which requires
³⁷¹ removing any non-negligible confounding effects [75].

372 Similarly, if R non-measurable (as is often the case), R must be estimated with proxies
373 such as NDVI [76], which may introduce complexities. While R and NDVI are correlated
374 for many species [e.g., 45,46,95,99–101], the relationship between the two can be weak [84],
375 satellite-dependent [85], and nonlinear [83,85]. This complexity can introduce two sources
376 of bias: ecosystem-level biases (indicated as Z in the directed acyclical graph in fig. 6)
377 and satellite-level confounding variables (S in fig. 6). Examples of ecosystem-level biases
378 are the effects of competition, predation, habitat connectivity, and movement costs, all of
379 which can depend on habitat quality, and, consequently, be correlated nonlinearly to R
380 and NDVI [35,102]. Resource-rich patches can attract larger amounts of competitors [14]
381 and predators [20], which may, in turn, increase pressures from competition and predation
382 [15,39]. However, such pressures may result in both an expansion of the range [35,102] or
383 a contraction, since larger ranges can be harder to defend and result in higher movement
384 costs [35,103] and encounter rates [104]. Satellite-level confounds include information loss
385 due to coarse spatiotemporal resolution [83,85], satellite-level error [83,85,105], and other
386 limitations of remote sensing (e.g., inability to quantify specific resources or small-scale
387 resource depletion). However, nonlinear models such as Generalized Additive Models [106]
388 can help account for preferences for intermediate values of remotely-sensed R [e.g., young
389 grass rather than mature grasslands, see 85].

390 **Conclusions**

391 The work presented here provides a unifying framework for viewing movement as a response
392 to resource abundance and stochasticity. We provide a sensible and unifying hypothesis
393 of the effects of $E(R)$ and $\text{Var}(R)$ on organisms' range sizes and movement behavior. We
394 demonstrate that organisms' range sizes decrease with resource abundance, increase with
395 resource stochasticity, and that the effects of $\text{Var}(R)$ can depend strongly on $E(R)$.

396 Recent advances in computational power have greatly increased analysts' ability to fit
397 computationally demanding models [107,108] that allow biologists to move beyond only

398 considering changes in mean conditions. By accounting for changes in stochasticity, we can
 399 start developing a more comprehensive understanding of how organisms adapt to the dynamic
 400 environments organisms live in, including recent changes in climate [109] and increases in
 401 the frequency and intensity of extreme events [66,67,110–112].

402 **List of abbreviations**

Abbreviation	Definition
H	Range size
$\hat{H}_{95\%}$	Estimated 95% home range size
C	Resource consumption rate
R	Resources
t	Moment in time
\vec{u}	Location in space (vector of coordinates)
$E(R)$	Resource abundance
$\mu(t)$	Resource abundance as a function of time
$\mu(t, \vec{u})$	Resource abundance as a function of time and space
$\text{Var}(R)$	Resource stochasticity
$\sigma^2(t)$	Resource stochasticity as a function of time
$\sigma^2(t, \vec{u})$	Resource stochasticity as a function of time and space
$\hat{\varsigma}^2$	Estimated positional variance
$\Gamma(\mu, \sigma^2)$	Gamma distribution with mean μ and variance σ^2
NDVI	Normalized Difference Vegetation Index
GAMLS	Generalized Additive Model for Location and Scale

⁴⁰⁴ **Declarations**

⁴⁰⁵ **Ethics approval and consent to participate**

⁴⁰⁶ Not applicable.

⁴⁰⁷ **Consent for publication**

⁴⁰⁸ Not applicable.

⁴⁰⁹ **Availability of data and materials**

⁴¹⁰ All code and data used for this manuscript is available on GitHub at <https://github.com/QuantitativeEcologyLab/hr-resource-stoch>, with the exception of two simulated datasets
⁴¹¹ that were greater than 100 MB and the tapir data. The simulated data can be produced
⁴¹² by running the scripts in the repository, while the tapir data is available at <https://github.com/StefanoMezzini/tapirs>.
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⁴¹⁴

⁴¹⁵ **Competing interests**

⁴¹⁶ The authors declare that they have no competing interests.

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⁴²² **Authors' contributions**

⁴²³ SM performed the literature review, designed the simulations, analyzed the data, and wrote
⁴²⁴ the manuscript. CHF contributed to the analyses. EPM provided the tapir telemetry data.

⁴²⁵ MJN conceived the project idea and provided support throughout the analyses. All authors
⁴²⁶ contributed to the writing and read and approved the final manuscript.

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