

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 organisms use is thought
³ to be tightly linked to the availability of resources within their habitats, such that organisms
⁴ living in productive habitats generally require less space than those in resource-poor habi-
⁵ tats. This hypothesis has widespread empirical support, but existing studies have focused
⁶ primarily on responses to spatiotemporal changes in mean resources, while responses to un-
⁷ predictable changes in resources (i.e., variance in resources or resource stochasticity) are still
⁸ largely unknown. Since organisms adjust to variable environmental conditions, failing to
⁹ consider the effects of resource unpredictability can result in an insufficient understanding
¹⁰ of an organism's range size. **Methods:** We leverage the available literature to provide a
¹¹ unifying framework and two hypotheses for the effects of resource abundance and stochas-
¹² ticity on organisms' range sizes. We then use simulated movement data to demonstrate how
¹³ the combined effects of resource abundance and stochasticity interact to shape predictable
¹⁴ patterns in range size. Finally, we test the two hypotheses using real-world tracking data
¹⁵ on a lowland tapir (*Tapirus terrestris*) from the Brazilian Cerrado. **Results:** Organisms'
¹⁶ range sizes decrease nonlinearly with resource abundance and increase nonlinearly with re-
¹⁷ source stochasticity, and the effects of resource stochasticity depend strongly on resource
¹⁸ abundance. Additionally, the distribution and predictability of resources can exacerbate
¹⁹ the effects of other drivers of movement, such as resource depletion, competition, and pre-
²⁰ dation. **Conclusions:** Accounting for resource abundance and stochasticity is crucial for
²¹ understanding the movement behavior of free-ranging organisms. Failing to account for re-
²² source stochasticity can lead to an incomplete and incorrect understanding of how and why
²³ 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 This individual will adopt different behaviors and adaptations if it lived in a desert with
65 equally scarce forage but rare, sudden, and strong pulses of resources (i.e., low mean and
66 high stochasticity). In the grassland, the grazer may require a large but constant home range
67 size as it moves between patches in search of food, while in the desert it may switch between
68 dispersal in search for high-resource patches and short-term range residency within patches

69 In this paper, we illustrate how an organism’s range size can be expected to depend on
70 both the abundance and unpredictability of resources. First, we set the theoretical back-
71 ground necessary for the successive sections by introducing key concepts and notation. Next,
72 we provide a review of the effects of resource abundance on range sizes while suggesting a
73 simple and unifying hypothesis. Afterwards, we provide a review of the effects of resource
74 stochasticity on organisms’ range sizes while suggesting a second simple and unifying hypoth-

75 esis. Subsequently, we support the two hypotheses using quantitative, simulated responses
76 in range size to changes in resource abundance and stochasticity. Finally, we demonstrate
77 how this framework can be used in practice to describe the movement ecology of a lowland
78 tapir (*Tapirus terrestris*) from the Brazilian Cerrado [29].

79 **Resources as a random variable**

80 Resources (e.g., food, water, shelter, heat) are often unpredictable (and difficult to quantify),
81 since they depend on various factors which cannot be accounted for easily, including climate
82 [7,30,31], weather [31,32], competitive pressure [33,34], and differences in energetics at among
83 individuals [7] and species [35]. Thus, we can treat the amount of resources R at a given
84 point in time (t) and space (location vector \vec{u}) as a random variable, denoted as $R(t, \vec{u})$.
85 Treating resources as a random variable allows us to leverage techniques from probability
86 theory and statistics, such as the expectation of a random variable (i.e., its mean) and its
87 variance around the mean. We indicate the expected value and variance of random variable
88 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
89 as functions of time (t) and space (\vec{u}). Appendix A defines and expands on the concepts
90 of probability distributions, expected value, variance, and provides examples of them for
91 Gamma and Beta distributions.

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

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

99 When $E(R)$ is high, we expect organisms' ranges to be relatively small and near the

100 smallest amount of space required to survive [see Fig. 1 as well as: 27,28,41]. Like Harestad
 101 and Bunnel [13], we also expect organisms' range sizes to increase nonlinearly as $E(R)$
 102 decreases, but we highlight that organisms may adopt different behaviors at low values of
 103 $E(R)$. These behaviors include maximal home range expansion [33,home range size is limited
 104 by vagility, habitat structure, competition, and predation, e.g., 34,42,43], migration [44–46],
 105 and nomadism [23,25,47,48]. It is unclear when organisms switch from range residency to
 106 migration or nomadism (or vice-versa), but understanding the gradient among these types
 107 of movement is necessary for quantifying the effect of resource abundance on organisms'
 108 range size and movement behavior [mammals: 49,moose, *Alces alces*: 23,eagles, *Haliaeetus*
 109 *leucocephalus*: 24,50,lesser flamingos, *Phoeniconaias minor*: 51]. Still, large-scale switches
 110 from range residency to nomadism (or vice-versa) are more likely to occur over evolutionary
 111 timescales rather than over an organism's lifespan (Fig. 1), since larger ranges require greater
 112 vagility, which, in turn, is facilitated by the development of morphological features such as
 113 hinged joints and elongated limbs [35,52–54].

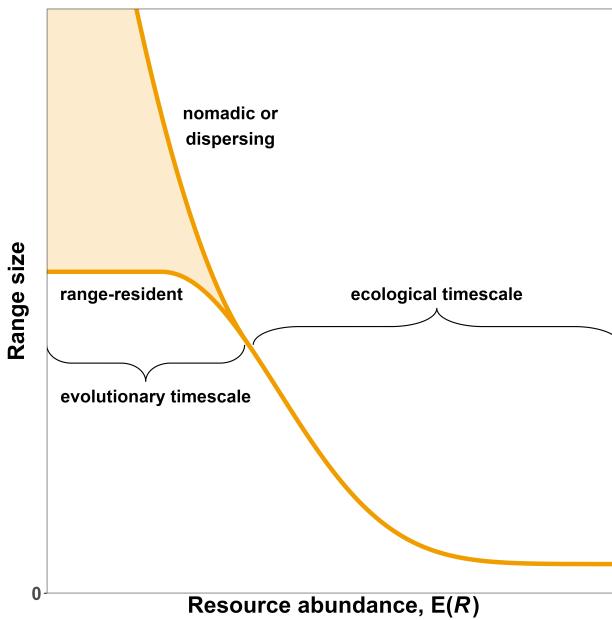


Figure 1: Hypothesized range size of an organism as a function of resource abundance, $E(R)$. We expect low values of $E(R)$ to result in a large range, since organisms are forced to explore large areas to collect the resources they require to survive, whether they be range-resident, nomadic, or migratory.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

¹¹⁴ Overall, the hypothesis that range size decreases with resource abundance, $E(R)$, is
¹¹⁵ commonly accepted and well supported, but many studies assume a linear relationship [e.g.,
¹¹⁶ 21,41,55–57]. This is problematic because, conceptually, the relationship between range size
¹¹⁷ and $E(R)$ must be nonlinear, since: (1) there is an upper limit to how much space an
¹¹⁸ organism is able to explore in its finite lifetime and (2) the minimum amount of space it
¹¹⁹ requires to survive is necessarily greater than zero [see 27,28,58,59,60, and contrast them to
¹²⁰ the earlier references that assume a linear relationship between H and R]. Consequently, we
¹²¹ suggest analysts use models that account for this nonlinearity when estimating the effects of
¹²² resource abundance on range size.

¹²³ Effects of resource stochasticity, $\text{Var}(R)$

¹²⁴ Assuming resource stochasticity is constant over time and space can be a useful simplification
¹²⁵ of relatively stable environments or when information on how $E(R)$ changes is limited and
¹²⁶ estimating changes in $\text{Var}(R)$ is unreasonable. However, such an assumption is likely not
¹²⁷ realistic, since $\text{Var}(R)$ often differ across space and over time. Generally, bounded quantities
¹²⁸ have correlated means and variances, as in the case of random variables that are strictly pos-
¹²⁹ itive (e.g., Gamma and Poisson) or fully bounded (e.g., Beta). For example, prey abundance
¹³⁰ in a given area over time may approximately follow a Poisson distribution, which implies
¹³¹ that the mean and variance will be approximately equal. When prey are scarce (e.g., a mean
¹³² of 10), the variance will also be low, and when prey are abundant (e.g., a mean of 300)
¹³³ the variance will also be high. This occurs because the behavior, fitness, and predator-prey
¹³⁴ dynamics of ~300 prey are more stochastic than those of 10 prey [61]. Similarly, in the
¹³⁵ case of fully bounded random variables, the variance is generally lowest when the mean is
¹³⁶ near either boundary. For example, successful predation events are predictably scarce if the
¹³⁷ probability of capture is near 0, predictably common if the probability is near 1, and most
¹³⁸ stochastic if the probability is near 0.5 [i.e., as far as possible from both 0 and 1; see [62]].

¹³⁹ See Appendix A for more information.

140 Recognizing changes in $\text{Var}(R)$ helps account for the residual, fine-scale variation in R
141 after accounting for trends in the large-scale average R [e.g., variations in plant phenology
142 between years after accounting for mean seasonal trends, see 63]. However, when both
143 $E(R)$ and $\text{Var}(R)$ change over time (fig. A2), disentangling changes in $E(R)$ and $\text{Var}(R)$ is
144 not simple [64]. Statistically, this confound occurs because the more change one attributes
145 to $\mu(t, \vec{u})$ (i.e., the wigglier it is), the smaller $\sigma^2(t, \vec{u})$ becomes. Conversely, the smoother
146 $\mu(t, \vec{u})$ is, the larger $\sigma^2(t, \vec{u})$ becomes. Biologically, it is important because an organism's
147 perception scale determines whether it attributes a change in R to a trend in $E(R)$ or as
148 a stochastic event [i.e., due to $\text{Var}(R)$; see [63]]. An organism's perception of changes in
149 R will also depend strongly on its cognitive capacities and memory [9,65–68]. Whether
150 an organism is able to predict trends in $\sigma^2(t, \vec{u})$ or not, environmental variability is thought
151 to reduce a landscape's energetic balance [26], which, in turn, decreases organisms' fitness
152 [e.g., 10] and increases their range size. While this behavioral response occurs with both
153 predictable and unpredictable stochasticity, extreme and rare events are more likely to have
154 a stronger effect due to their unpredictability and magnitude [69,70]. A few recent studies
155 support these hypotheses [22,26,31,48,71], but many of them are limited in geographic and
156 taxonomic scales or fail to account for nonlinear relationships, so the extent to which these
157 preliminary findings can be generalized is currently unknown. Thus, there remains a need
158 for developing a more complete understanding of how organisms' range sizes changes with
159 environmental stochasticity.

160 Similarly to $E(R)$, we hypothesize $\text{Var}(R)$ has a nonlinear effect on an organism's range
161 size. When $\text{Var}(R)$ is low enough that R is relatively predictable, we expect organisms to be
162 range-resident with small home ranges, and we do not expect small changes in $\text{Var}(R)$ to have
163 a noticeable effect. As resources become increasingly unpredictable, we expect home range
164 size to increase progressively faster (fig. 2) because: (1) as $\text{Var}(R)$ increases, the chances of
165 finding low R increase superlinearly, (2) the added movement required to search for food
166 increases organisms' energetic requirements, and (3) stochasticity reduces an organism's abil-

ity to specialize and reduce competition for R [72]. 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., 73].

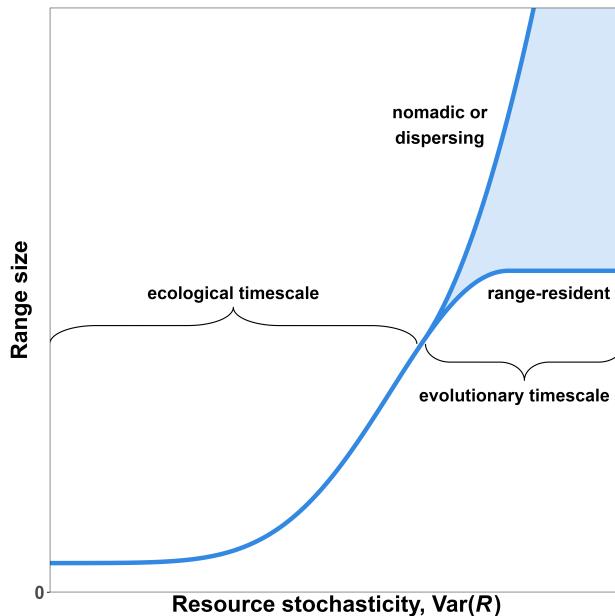


Figure 2: Hypothesized range size of an organism as a function of resource stochasticity, $\text{Var}(R)$. We expect low values of $\text{Var}(R)$ to result in small home-ranges, since organisms are able to depend on relatively predictable resources. As $\text{Var}(R)$ increases, range size should increase 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 $\text{Var}(R)$.

174 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 likely to be a function of not only the marginal effects of $E(R)$ and $\text{Var}(R)$ but also their

180 interactive effects. A highly unpredictable habitat may be very inhospitable if resources
181 are poor, but $\text{Var}(R)$ may have little effect if resources are stochastic but always abundant.
182 Thus, we expect $\text{Var}(R)$ to have a stronger effect on range size when $E(R)$ is low, and less of
183 an effect when $E(R)$ is high. We explore this interaction effect more in the following section.

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

185 To support our hypotheses of how organisms' range sizes are affected by $E(R)$, $\text{Var}(R)$, and
186 the interaction effect of $E(R)$ and $\text{Var}(R)$, we present the results from a series of quantitative
187 simulations. To start, we used the `ctmm` package [74] for `R` [75] to generate 200 tracks
188 (see Appendix B for sensitivity analyses) from an Integrated Ornstein-Uhlenbeck movement
189 model [IOU model, see 76]. The IOU model's correlated velocity produced realistic tracks
190 with directional persistence, but, unlike Ornstein-Uhlenbeck (OU) and Ornstein-Uhlenbeck
191 Foraging (OUF) models, IOU models do not produce spatially stationary movement, so the
192 organism is not to range-resident. Consequently, each track is spatially unrestricted and can
193 be interpreted as purely exploratory or memoryless movement.

194 Each of the 200 tracks were placed on a grid with common starting point $\langle 0, 0 \rangle$ (fig. B1).
195 Each time the simulated individual moved to a new cell, it collected R resources sampled
196 from a Gamma distribution. The mean and variance of the distribution were defined by a
197 series of deterministic functions $\mu(t)$ and $\sigma^2(t)$ (orange and blue lines in fig. 3). The value
198 of t was constant within each set of 200 tracks, so the distribution R was sampled from
199 was independent of both the organism's location and its time spent moving. Tracks were
200 truncated once the organism reached satiety, and the organism was given enough time to
201 return to $\langle 0, 0 \rangle$ independently from the following track (section 2.1 of Appendix B). Finally,
202 we fit an OUF movement model [77] to the set of tracks to calculate the 95% Gaussian
203 home-range size using the formula

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

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

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

- 208 1) Environments are homogeneous for a given t . Given t , $E(R) = \mu(t)$ and $\text{Var}(R) = \sigma^2(t)$
209 are constant over space and within each set of 200 tracks, but R is random and follows
210 a $\Gamma(\mu(t), \sigma^2(t))$ distribution.
- 211 2) There are no external pressures on the simulated organism. Resources do not deplete,
212 and there is no competition nor predator avoidance.
- 213 3) The organism has a fixed daily energetic requirement that is independent of movement
214 rates, and it cannot alter its metabolism or physiology. Additionally, the organism
215 does not have energetic reserves, so excess resources cannot be carried over to the next
216 track or t .
- 217 4) The organism is range-resident and can only respond to changes in $E(R)$ and $\text{Var}(R)$
218 by altering its home-range size. The organism does not disperse or abandon a range.
- 219 5) The organism's movement is simplistic. The organism's movement speed and direction
220 are stochastic and independent of $E(R)$ and $\text{Var}(R)$.
- 221 6) The organism has no perceptive range or memory. It is unable to detect, learn, or
222 predict where resources are abundant (high $E(R)$) or reliable (low $\text{Var}(R)$) over time
223 or space.
- 224 7) Animals only move to search for food or return to the center of their home-range after
225 reaching satiety.

226 Additional information is provided in Appendix B, including the directed acyclical graph
227 [see fig. B6 and 78] we used to infer causal mechanisms of changes in H and estimate the
228 direct effects of $E(R)$ and $\text{Var}(R)$ on H (contrast the graph with fig. C3 and the empirical
229 case study below).

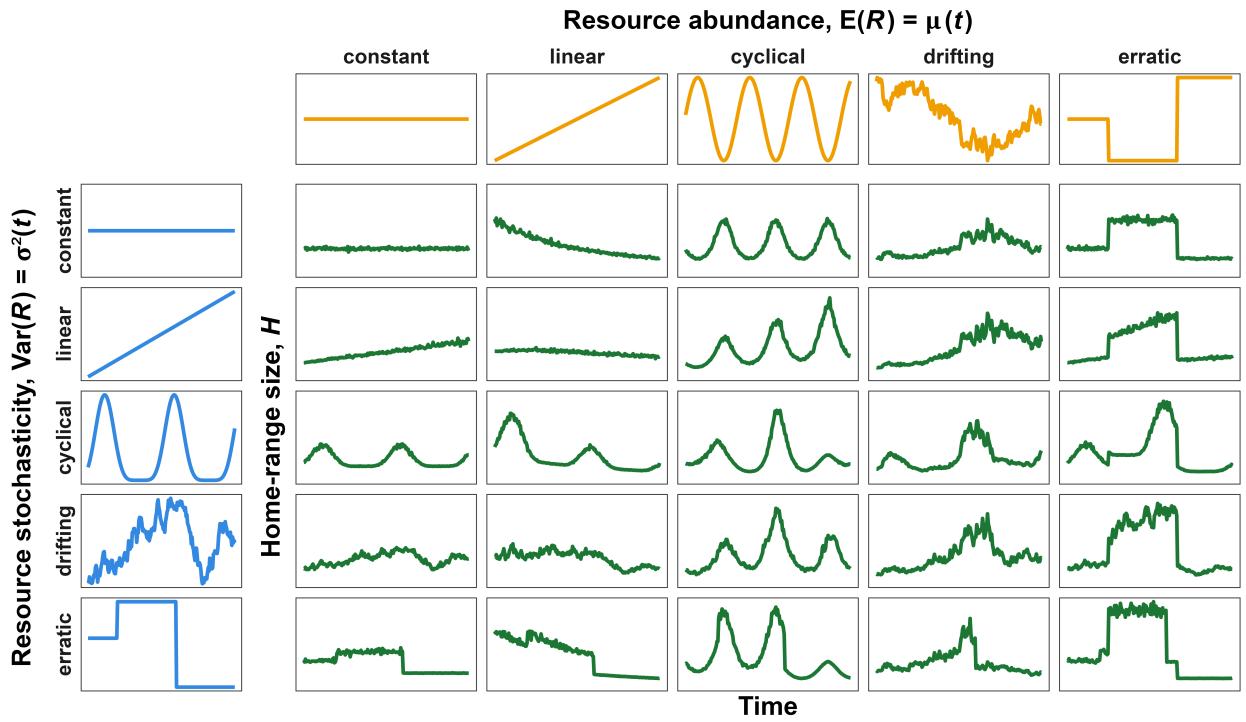


Figure 3: Simulated home-range sizes, H , of an organism living in habitats where the mean and variance in resources are constant, linearly increasing, cyclical, drifting, or erratic over time (but homogeneous over space for a given t). Note how H decreases nonlinearly as $\mu(t)$ increases and increases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

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

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

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

251 Although the temporal trends in fig. 3 are complex and the effects of $E(R)$ and $\text{Var}(R)$
252 can be hard to disentangle, two simple relationships emerge when H is shown as a function
253 of either $E(R)$ or $\text{Var}(R)$, rather than time (panels A and B of fig. 4). The estimated
254 relationships follow the hypotheses we presented in figs. 1 and 2, although we found that the
255 effect of $\text{Var}(R)$ at average $E(R)$ was linear with a slight sublinear saturation at high values
256 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.

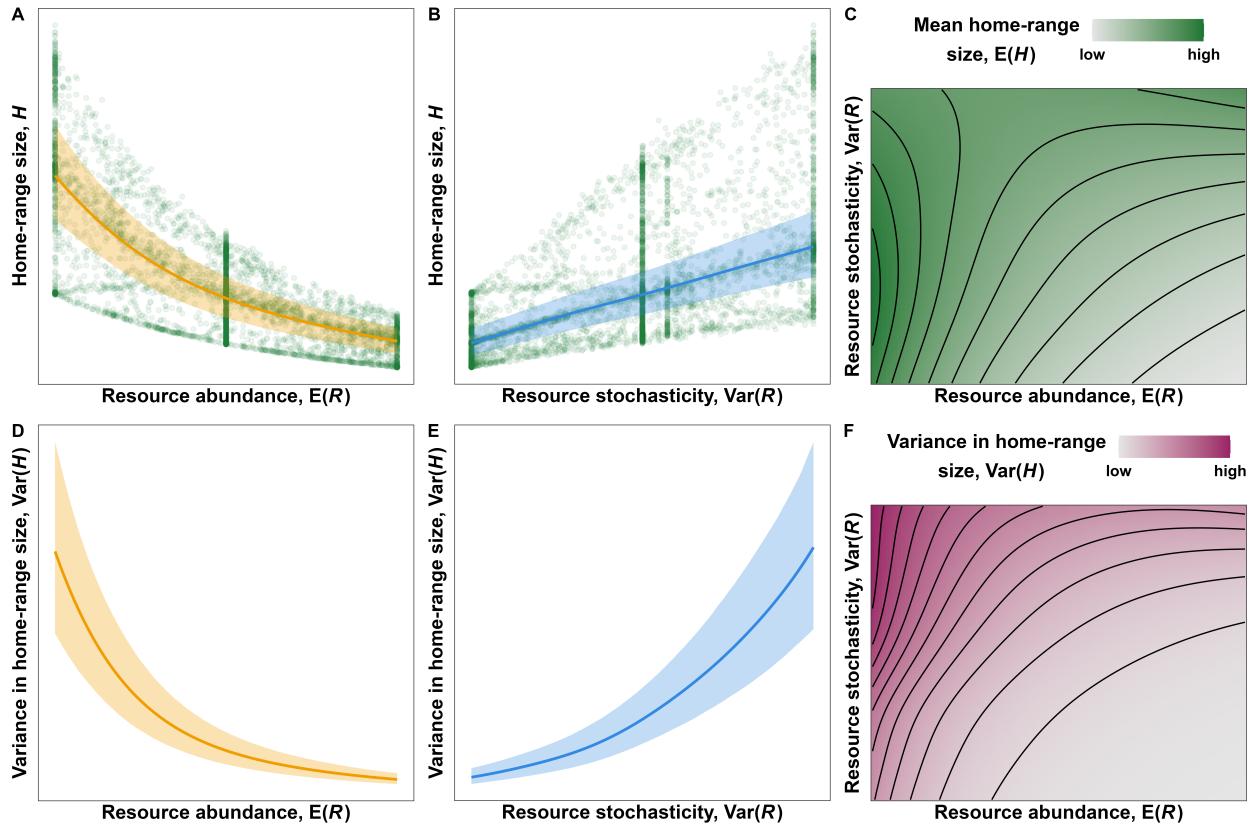


Figure 4: Effects of $E(R)$ and $\text{Var}(R)$ on the mean (A-C) and variance (D-F) in simulated home-range size with 95% Bayesian credible intervals. While the estimated marginal effect of $\text{Var}(R)$ on $E(H)$ is sublinear (panel B), the effect of $\text{Var}(R)$ is superlinear for high values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

268 The simulations in the section above support the hypotheses we presented in the background
269 section, but they are based on assumptions that are often not met in real natural environments.
270 Organisms live in spatiotemporally heterogeneous and dynamic environments that
271 promote the use of perceptual ranges, navigation, and memory. Together, these abilities
272 result in selective space use that depends on resource availability [14] and resource depletion
273 [15].

274 In this section, we test the hypotheses using empirical tracking data on a lowland tapir
275 from the Brazilian Cerrado along with empirical estimates of $E(R)$ and $\text{Var}(R)$. We measure
276 R using Normalized Difference Vegetation Index [NDVI, see 79], a remote-sensed measure
277 of landscape greenness, as a proxy for forage abundance. Appendix C contains additional
278 information on how we modeled NDVI and the tapir’s movement using continuous-time
279 movement models [74,80] and autocorrelated kernel density estimation [81–83].

280 Fig. 5 illustrates how a tapir in the Brazilian Cerrado adapts its 7-day home-range
281 size to spatiotemporal changes in estimated $\mu(t, \vec{u})$ and $\sigma^2(t, \vec{u})$ (telemetry data from the
282 individual labelled as “Anna” in the dataset from [29]). Panels A and B show the changes in
283 seven-day average mean and variance in NDVI, respectively, experienced by the tapir during
284 the tracking period. The mean and variance in NDVI were estimated using a Generalized
285 Additive Model for Location and Scale [GAMLS, 84] with a Beta family of distributions
286 (NDVI values ranged from 0.3534 to 0.9475). Panel C shows the changes in the tapir’s
287 7-day home range over time. Note how the tapir uses more space during periods of lower
288 NDVI (e.g., August 2017) and less space during periods with high NDVI (January 2018).
289 Additionally, when resources are scarce and highly unpredictable (August 2018), the tapir
290 uses up to 5 times more space than when resources are abundant and predictable (e.g.,
291 January 2018). Finally, panels D and E show the estimated (marginal) effects of $\hat{\mu}(t, \vec{u})$ and
292 $\hat{\sigma}^2(t, \vec{u})$ on the tapir’s 7-day home-range size. Since $\hat{\mu}(t, \vec{u})$ and $\hat{\sigma}^2(t, \vec{u})$ are correlated (panel

293 F) and spatiotemporally autocorrelated (panels A, B, and F), the effects of R on H should
294 be modeled carefully. To avoid over-fitting the model, we constrained the smooth effects
295 of $\hat{\mu}(t, \vec{u})$ and $\hat{\sigma}^2(t, \vec{u})$ and their interaction effect to a small basis size ($k = 3$). Additional
296 information is provided in appendix C. The results presented in panels D-F of fig. 5 match
297 our findings from the simulations: The tapir's 7-day home range decreases with $\hat{\mu}(t, \vec{u})$ and
298 increases with $\hat{\sigma}^2(t, \vec{u})$, and the effect of $\hat{\mu}(t, \vec{u})$ depends on $\hat{\sigma}^2(t, \vec{u})$, and vice-versa. Alone,
299 $\hat{\mu}(t, \vec{u})$ and $\hat{\sigma}^2(t, \vec{u})$ cause the tapir to double her home range (panels D and E), but together
300 they result in an approximate 15-fold change in home-range size (observed range: 0.8 to 12.4
301 km²; see panel F). Additionally, note how high NDVI values ($\hat{\mu}(t, \vec{u}) > 0.8$) cause $\hat{\sigma}^2(t, \vec{u})$ to
302 have little to no effect on home-range size, as indicated by the vertical contour line in panel
303 F.

304 Discussion

305 The amount of space organisms use is determined by a multitude of factors [16], but the
306 search for resources is often a main driver of animal how much and where organisms move.
307 This paper builds on earlier theoretical work [13,e.g., 18,19] and presents two hypotheses
308 that describe the effects of resource abundance and stochasticity on organisms' range sizes.
309 We use quantitative simulations and an empirical case study to support the hypotheses
310 and show that, together, they provide a simple framework for understanding how motile
311 organisms adapt their movement in dynamic environments. Separately, resource abundance
312 and stochasticity have simple but opposing effects on organisms' range sizes: H decreases
313 with $E(R)$ and increases with $\text{Var}(R)$. Together, the degree to which $E(R)$ affects H depends
314 on $\text{Var}(R)$, and vice-versa, so organisms' responses to resource dynamics can be complex.
315 The simulated and empirical results suggest qualitatively similar marginal effects of $E(R)$
316 and $\text{Var}(R)$, but there are differences in the estimated interactive effects. In the simulated
317 data, $\text{Var}(R)$ has little effect when $E(R)$ is low and a strong effect when $E(R)$ is high, while
318 the opposite is true for the empirical data. This difference is due to two reasons. Firstly, the

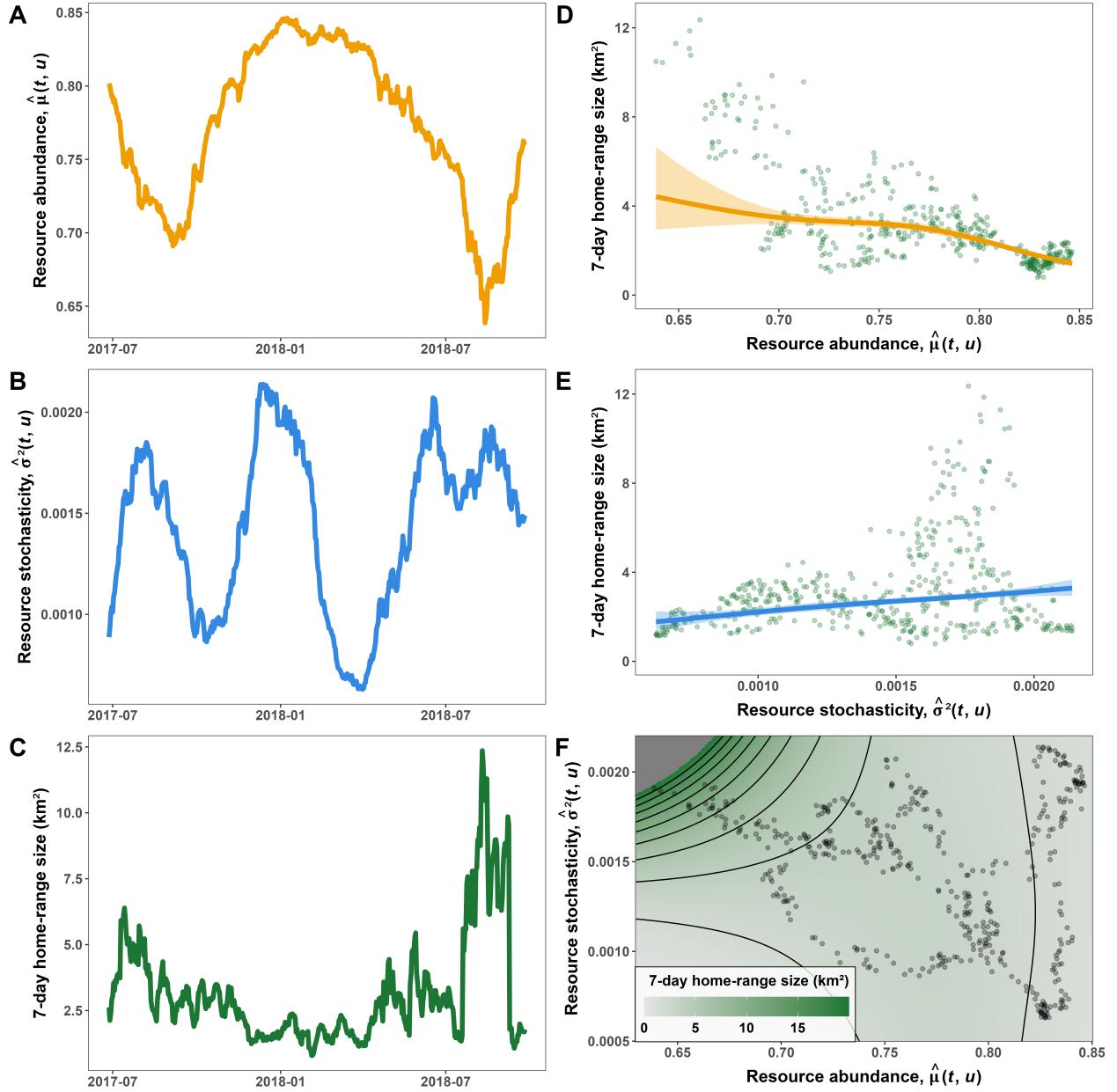


Figure 5: Effects of estimated $\mu(t, \bar{u})$ and $\sigma^2(t, \bar{u})$ on the home-range size of a lowland tapir (*Tapirus terrestris*). (A) Trends in resource abundance over time, $\hat{\mu}(t, \bar{u})$, estimated as the average mean NDVI at the locations visited by the tapir during a seven-day 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.* [27].

319 shape and symmetry of bounded distributions such as Gamma ($R > 0$) and Beta ($0 < R < 1$)
320 distributions depend on both $E(R)$ and $\text{Var}(R)$ (figs. A3, A4), but $\text{Var}(R)$ does not affect
321 the shape of a Gamma distribution as much if $E(R)$ is low (fig. B3). Secondly, and perhaps
322 more interestingly, the simulation approach does not account for real-world adaptations to
323 $E(R)$ and $\text{Var}(R)$ such as selective space use, which we account for in the empirical approach.
324 Below we discuss the strengths and limitations of each approach.

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

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

335 Deviations from the simulations offer a means of detecting when the underlying assump-
336 tions are inappropriate and how additional factors may affect organisms' responses to changes
337 in $E(R)$ and $\text{Var}(R)$. For example, energetic costs of movement are often non-negligible and
338 depend on organism size [40], movement speed [40], and ambient temperature [1,85]. In addi-
339 tion, an organism may alter its movement behavior, physiology, and energetic needs to buffer
340 itself against changes in $E(R)$ and $\text{Var}(R)$ by using space selectively [71,86–88] and adapting
341 their behavior and physiology over time [18,72]. Before or during periods of scarcity, organ-
342 isms may cache resources [89], build up fat reserves [45], enter states of dormancy [90–92],
343 or even pause fetal growth [7]. However, organisms may be unable to respond to changes
344 in $E(R)$ and $\text{Var}(R)$ optimally due to various reasons, including limited perceptive range

[64], lack of experience [9,47,66–68,93], avoidance of competitors and predators [14,94], or a physiology that is not amenable to things like hibernation or fat storage. Thus, organisms may relocate their range to a sub-optimal location [33,34,95,96], which may exacerbate the effects of $E(R)$ and $\text{Var}(R)$ on both mean range size and the variance around it.

Strengths and limitations of the empirical approach

There are two main advantages of taking an empirical approach. Firstly, modeling real-world animal movement data can produce scale-appropriate and easily interpretable estimates. Secondly, empirical models directly quantify the effects of $E(R)$, $\text{Var}(R)$, and confounding variables without having to design complex and time-consuming simulations. However, it is not always possible to quantify confounding variables. For example, while there may be some appropriate proxies of competition, such as density of competitors, these variables may be hard to quantify, and they may not account for the confounding effects appropriately (i.e., the presence of competitors may not reflect competitive pressure). This is problematic if one is interested in estimating the direct causal effect of $E(R)$ and $\text{Var}(R)$, which requires removing any non-negligible confounding effects [78].

Similarly, if R is often non-measurable. Proxies of R , such as NDVI [79], which may introduce complexities. While R and NDVI are correlated for many species [e.g., 45,46,93,97–99], the relationship between the two can be weak [100], satellite-dependent [101], and nonlinear [101,102]. This complexity can introduce two sources of bias: ecosystem-level biases (indicated as Z in the directed acyclical graph in fig. C3) and satellite-level confounding variables (S in fig. C3). Examples of ecosystem-level biases are the effects of competition, predation, habitat connectivity, and movement costs, all of which can depend on habitat quality, and, consequently, be correlated nonlinearly to R and NDVI [35,103]. Resource-rich patches can attract larger amounts of competitors [14] and predators [20], which may, in turn, increase pressures from competition and predation [15,39]. However, such pressures may result in both an expansion of the range [35,103] or a contraction, since larger ranges can be harder

371 to defend and result in higher movement costs [35,104] and encounter rates [105]. Satellite-
372 level confounds include information loss due to coarse spatiotemporal resolution [101,102],
373 satellite-level error [101,102,106], and other limitations of remote sensing (e.g., inability to
374 quantify specific resources or small-scale resource depletion). However, nonlinear models
375 such as Generalized Additive Models [107] can help account for preferences for intermediate
376 values of remotely-sensed R [e.g., young grass rather than mature grasslands, see 101].

377 Conclusions

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

383 Recent advances in computational power have greatly increased analysts' ability to fit
384 computationally demanding models [108,109] that allow biologists to move beyond only
385 considering changes in mean conditions. By accounting for changes in stochasticity, we can
386 start developing a more comprehensive understanding of how organisms adapt to the dynamic
387 environments organisms live in, including recent changes in climate [110] and increases in
388 the frequency and intensity of extreme events [69,70,111–113].

³⁸⁹ **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
³⁹⁰ $\mu(t)$	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
$\hat{\zeta}^2$	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

³⁹¹ **Declarations**

³⁹² **Ethics approval and consent to participate**

³⁹³ Not applicable.

³⁹⁴ **Consent for publication**

³⁹⁵ Not applicable.

396 **Availability of data and materials**

397 All code and data used for this manuscript is available on GitHub at <https://github.com/>
398 QuantitativeEcologyLab/hr-resource-stoch, with the exception of two simulated datasets
399 that were greater than 100 MB and the tapir data. The simulated data can be produced
400 by running the scripts in the repository, while the tapir data is available at <https://github.com/StefanoMezzini/tapirs>.
401

402 **Competing interests**

403 The authors declare that they have no competing interests.

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409 **Authors' contributions**

410 SM performed the literature review, designed the simulations, analyzed the data, and wrote
411 the manuscript. CHF contributed to the analyses. EPM provided the tapir telemetry data.
412 MJN conceived the project idea and provided support throughout the analyses. All authors
413 contributed to the writing and read and approved the final manuscript.

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