

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
5 empirical support, but existing studies have focused primarily on responses to the mean
6 amount of resources, while responses to the variance around the mean are still largely un-
7 known. Since organisms adjust to variable environmental conditions, failing to consider
8 the effects of resource (un)predictability can result in an insufficient understanding of an
9 organism's range size, which results in challenges for both ecological theory and applied con-
10 servation. In this study, we leverage the available literature to provide a unifying framework
11 and two hypotheses for the effects of resource abundance and stochasticity on range sizes.
12 Next, we use simulated movement data to demonstrate how the combined effects of mean
13 and variance in resources 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 [1,2], altered physiology
₂₁ [2–5], lower chance of reproduction [2,6–8], and even death [9,10]. Thus, many organisms
₂₂ adapt their behaviors and/or physiology in response to changes in local resource abundance
₂₃ to ensure their needs are met.

₂₄ While there are many ways that individuals can respond to resource availability, move-
₂₅ ment represents one of the most readily available traits that species can adjust [11–13]. The
₂₆ relationship between organisms' movement and resource abundance has long been of inter-
₂₇ est to biologists. In his seminal paper, [14] considered the search for food as the primary
₂₈ driver for movement within an organism's home range. Three decades after, [15] suggested
₂₉ that change in resource abundance drives how organisms decide where to live and when to
₃₀ reproduce. Two years later, [16] proposed that the simplest relationship between resource
₃₁ abundance and an organism's home-range size is

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

₃₂ where H is the organism's home-range size, C is the organism's resource consumption (kcal
₃₃ day $^{-1}$), and R is the resources the organism can access (kcal day $^{-1}$ unit area $^{-1}$). Harestad
₃₄ and Bunnel's model is simple to conceptualize, and it allows for testable predictions, but few
₃₅ studies are structured around a set of theoretical expectations such as Harestad and Bunnel's
₃₆ hypothesis. Many researchers have since demonstrated that organisms adapt their range sizes
₃₇ in response to resources abundance, but results are typically reported as independent, novel
₃₈ findings. Perhaps more problematic is the fact that, while much work has been done on
₃₉ estimating organisms' responses to mean resource abundance, there is little information on
₄₀ how organisms respond to variance around the mean [i.e., resource stochasticity, but see:

41 17,18–20]. Thus, there remains a need for clear hypotheses of the effects of both resource
42 abundance and stochasticity on organisms’ range sizes.

43 Here, we refer to a location’s average amount of resources as “resource abundance”,
44 while we use the phrase “resource stochasticity” to indicate the variability in resources after
45 accounting for changes in the mean. We argue that, on its own, a habitat’s resource abun-
46 dance is not sufficient to assess the habitat’s quality, nor make predictions about how much
47 space an organism might use. To see this, consider, for instance, a herbivore grazing in a
48 grassland with relatively low but constant forage availability (i.e., low mean and variance).
49 This individual will adopt different behaviors and adaptations if it lived in a desert with
50 equally scarce forage but rare, sudden, and strong pulses of resources (i.e., low mean and
51 high stochasticity). In the grassland, the grazer may require a large but constant home
52 range size as it moves between patches in search of food, while in the desert it may switch
53 between dispersal in search for high-resource patches and short-term range residency within
54 patches [*sensu* 12,see 21,22,23]. Previous studies suggest that resource stochasticity may
55 decrease organisms’ fitness and landscapes’ energetic balances [e.g., 24], but there is still
56 limited empirical evidence to support this hypothesis [19, but see: 25,26].

57 In this paper, we illustrate how an organism’s range size can be expected to depend on
58 both the abundance and unpredictability of resources. First, we set the theoretical back-
59 ground necessary for the successive sections by introducing key concepts and notation. Next,
60 we provide a review of the effects of resource abundance on range sizes while suggesting a
61 simple and unifying hypothesis. Afterwards, we provide a review of the effects of resource
62 stochasticity on organisms’ range sizes while suggesting a second simple and unifying hypoth-
63 esis. Subsequently, we support the two hypotheses using quantitative, simulated responses
64 in range size to changes in resource abundance and stochasticity. Finally, we demonstrate
65 how this framework can be used in practice to describe the movement ecology of a lowland
66 tapir (*Tapirus terrestris*) from the Brazilian Cerrado [27].

67 **Resources as a random variable**

68 Resources are often unpredictable (and difficult to quantify), since they depend on various
69 factors which cannot be accounted for easily, including climate [7,28,29], weather [29,30],
70 competitive pressure [31,32], and differences in energetics at among individuals [7] and species
71 [33]. Thus, we can treat the amount of resources R at a given point in time (t) and space
72 (location vector \vec{u}) as a random variable, denoted as $R(t, \vec{u})$. Treating resources as a random
73 variable allows us to leverage techniques from probability theory and statistics, such as the
74 expectation of a random variable (i.e., its mean) and its variance around the mean. We
75 indicate the expected value and variance of random variable R using $E(R)$ and $\text{Var}(R)$,
76 respectively, and we use $\mu(t, \vec{u})$ and $\sigma^2(t, \vec{u})$ to indicate them as functions of time (t) and
77 space (\vec{u}). Appendix A defines and expands on the concepts of probability distributions,
78 expected value, variance, and provides examples of them for gamma and beta distributions.

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

80 While organisms' needs vary greatly between taxonomic groups, some needs are essential
81 for the growth, survival, and reproduction of most organisms. All heterotrophic organisms
82 require sources of chemical energy (i.e., food), water, and various limiting nutrients [34–
83 36]. As the abundance of essential resources fluctuates, motile organisms can move to new
84 locations or 'patches' to meet their requirements [12,37], but they must also account for costs
85 of movement [38].

86 Fig. 1 illustrates our first of two hypotheses, which is similar to that presented by
87 [16]. When $E(R)$ is high, we expect organisms' ranges to be relatively small and near
88 the smallest amount of space required to survive [25,26,e.g., 39]. Like [16], we also expect
89 organisms' range sizes to increase nonlinearly as $E(R)$ decreases, but we highlight that
90 organisms may adopt different behaviors at low values of $E(R)$. These behaviors include
91 maximal home range expansion [31,home range size is limited by vagility, habitat structure,

92 competition, and predation, e.g., 32,40,41], migration [42–44], and nomadism [21,23,45,46].
 93 It is unclear when organisms switch from range residency to migration or nomadism (or
 94 vice-versa), but understanding the gradient among these types of movement is necessary
 95 for quantifying the effect of resource abundance on organisms' range size and movement
 96 behavior [mammals: 47, moose, *Alces alces*: 21, eagles, *Haliaeetus leucocephalus*: 22,48, lesser
 97 flamingos, *Phoeniconaias minor*: 49]. Still, switches from range residency to nomadism (or
 98 vice-versa) will occur over evolutionary timescales rather than over an organism's lifespan
 99 (Fig. 1), since larger ranges require greater vagility, which, in turn, is facilitated by the
 100 development of morphological features such as hinged joints and elongated limbs [33,50–52].

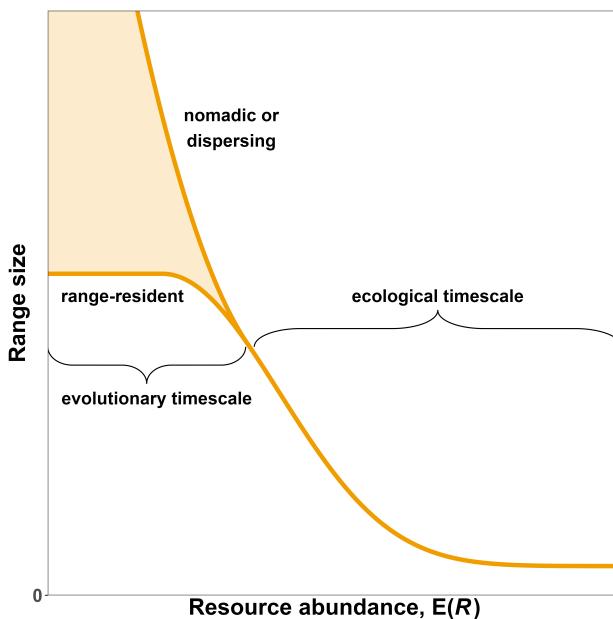


Figure 1: Hypothesized range size of an organism as a function of resource abundance, $E(R)$. We expect low values of $E(R)$ to result in a large range, since organisms are forced to explore large areas to collect the resources they require to survive, whether they be range-resident, nomadic, or migratory.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

101 Overall, the hypothesis that range size decreases with resource abundance, $E(R)$, is com-
 102 monly accepted and well supported, but many studies assume a linear relationship [19,e.g.,
 103 39,53–55]. This is problematic because, conceptually, the relationship between range size
 104 and $E(R)$ must be nonlinear, since: (1) there is an upper limit to how much space an organ-
 105 ism is able to explore in its finite lifetime and (2) the minimum amount of space it requires

106 to survive is necessarily greater than zero [25,26,see: 56,57,58, and contrast them to the
107 estimates based on linear models listed above]. Consequently, we suggest analysts use mod-
108 els that account for this nonlinearity when estimating the effects of resource abundance on
109 range size.

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

111 Assuming resource stochasticity is constant over time and space can be a useful simplification
112 of relatively stable environments or when information on how $E(R)$ changes is limited and
113 estimating changes in $\text{Var}(R)$ is unreasonable. However, such an assumption is likely not
114 realistic, since $\text{Var}(R)$ often differ across space and over time. Generally, bounded qualities
115 quantities have correlated means and variances, as in the case of random variables that are
116 strictly positive (e.g., Gamma and Poisson) or fully bounded (e.g., beta). See Appendix A
117 for more information.

118 Recognizing changes in $\text{Var}(R)$ helps account for the residual, fine-scale variation in R
119 after accounting for trends in the large-scale average R [e.g., variations in plant phenology
120 between years after accounting for mean seasonal trends, see 59]. However, when both
121 $E(R)$ and $\text{Var}(R)$ change over time (fig. A2), disentangling changes in $E(R)$ and $\text{Var}(R)$ is
122 not simple [60]. Statistically, this confound occurs because the more change one attributes
123 to $\mu(t, \vec{u})$ (i.e., the wigglier it is), the smaller $\sigma^2(t, \vec{u})$ becomes. Conversely, the smoother
124 $\mu(t, \vec{u})$ is, the larger $\sigma^2(t, \vec{u})$ becomes. Biologically, it is important because an organism's
125 perception scale determines whether it attributes a change in R to a trend in $E(R)$ or as
126 a stochastic event [i.e., due to $\text{Var}(R)$; see [59]]. An organism's perception of changes in
127 R will also depend strongly on the its cognitive capacities and memory [9,61–64]. Whether
128 an organism is able to predict trends in $\sigma^2(t, \vec{u})$ or not, environmental variability is thought
129 to reduce a landscape's energetic balance [24], which, in turn, decreases organisms' fitness
130 [e.g., 10] and increases their range size. While this behavioral response occurs with both
131 predictable and unpredictable stochasticity, extreme and rare events are more likely to have

132 a stronger effect due to their unpredictability and magnitude [65,66]. A few recent studies
133 support these hypotheses [20,24,29,46,67], but many of them are limited in geographic and
134 taxonomic scales or fail to account for nonlinear relationships, so the extent to which these
135 preliminary findings can be generalized is currently unknown. Thus, there remains a need
136 for developing a more complete understanding of how organisms' range sizes changes with
137 environmental stochasticity.

138 Similarly to $E(R)$, we hypothesize $\text{Var}(R)$ has a nonlinear effect on an organism's range
139 size. When $\text{Var}(R)$ is low enough that R is relatively predictable, we expect organisms to be
140 range-resident with small home ranges, and we do not expect small changes in $\text{Var}(R)$ to have
141 a noticeable effect. As resources become increasingly unpredictable, we expect home range
142 size to increase progressively faster (fig. 2) because: (1) as $\text{Var}(R)$ increases, the chances of
143 finding low R increase superlinearly, (2) the added movement required to search for food
144 increases organisms' energetic requirements, and (3) stochasticity reduces an organism's abil-
145 ity to specialize and reduce competition for R [68]. If resources remain highly unpredictable
146 over long periods of time (e.g., multiple lifespans), organisms may evolve or develop new
147 and consistent behaviors (e.g., nomadism) or adaptations (e.g., increased fat storage or food
148 caching) to buffer themselves against times of unpredictably low R . Conversely, if changes
149 in $\sigma^2(t, \vec{u})$ are sufficiently predictable, organisms may learn to anticipate and prepare for
150 times of greater stochasticity by pre-emptively caching food, reducing energetic needs,
151 migrating, or relying on alternative food sources [e.g., 69].

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

153 We have provided the case for why both $E(R)$ and $\text{Var}(R)$ should be expected to affect
154 organisms' range size, but we presented the two parameters as independent drivers of move-
155 ment. However, organisms may respond to changes in $\sigma^2(t, \vec{u})$ more when resources are
156 scarce than when they are abundant. Consequently, an organism's movement behavior is
157 likely to be a function of not only the marginal effects of $E(R)$ and $\text{Var}(R)$ but also their

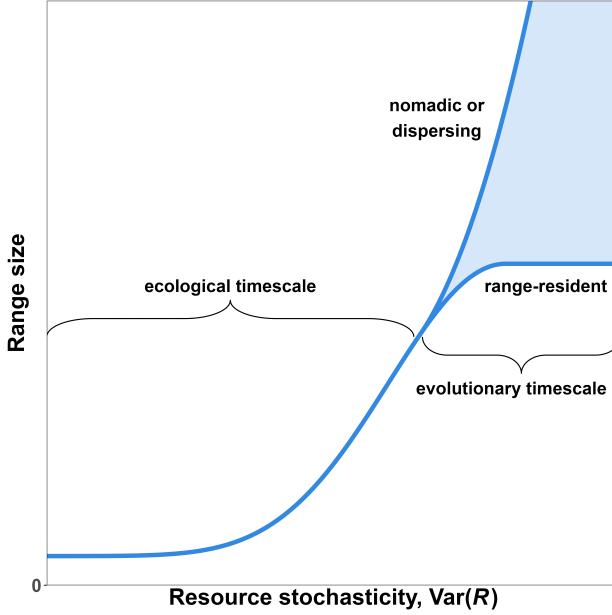


Figure 2: Hypothesized range size of an organism as a function of resource stochasticity, $\text{Var}(R)$. We expect low values of $\text{Var}(R)$ to result in small home-ranges, since organisms are able to depend on relatively predictable resources. As $\text{Var}(R)$ increases, range size should increase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

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

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

163 To support our hypotheses of how organisms' range sizes are affected by $E(R)$, $\text{Var}(R)$, and
 164 the interaction effect of $E(R)$ and $\text{Var}(R)$, we present the results from a series of quantitative
 165 simulations. To start, we used the `ctmm` package [70] for R [71] to generate 200 tracks
 166 (see Appendix B for sensitivity analyses) from an Integrated Ornstein-Uhlenbeck movement
 167 model [IOU model, see 72]. The IOU model's correlated velocity produced realistic tracks
 168 with directional persistence, but, unlike Ornstein-Uhlenbeck (OU) and Ornstein-Uhlenbeck
 169 Foraging (OUF) models, IOU models do not produce spatially stationary movement, so the
 170 organism is not to range-resident. Consequently, each track is spatially unrestricted and can

₁₇₁ be interpreted as purely exploratory or memoryless movement.

₁₇₂ Each of the 200 tracks were placed on a grid with common starting point $\langle 0, 0 \rangle$ (fig. B1).

₁₇₃ Each time the simulated individual moved to a new cell, it collected R resources sampled

₁₇₄ from a Gamma distribution. The mean and variance of the distribution were defined by a

₁₇₅ series of deterministic functions $\mu(t)$ and $\sigma^2(t)$ (orange and blue lines in fig. 3). The value

₁₇₆ of t was constant within each set of 200 tracks, so the distribution R was sampled from

₁₇₇ was independent of both the organism's location and its time spent moving. Tracks were

₁₇₈ truncated once the organism reached satiety, and the organism was given enough time to

₁₇₉ return to $\langle 0, 0 \rangle$ independently from the following track (section 2.1 of Appendix B). Finally,

₁₈₀ we fit an OUF movement model [73] to the set of tracks to calculate the 95% Gaussian

₁₈₁ home-range size using the formula

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

₁₈₂ where $\hat{\zeta}^2$ is the positional variance estimated by the movement model.

₁₈₃ We designed the simulations to estimate the effects of $E(R)$ and $\text{Var}(R)$ in simplistic

₁₈₄ environments where organisms could only respond by searching for longer periods of time.

₁₈₅ Consequently, we made the following assumptions:

₁₈₆ 1) Environments are homogeneous for a given t . Given t , $E(R) = \mu(t)$ and $\text{Var}(R) = \sigma^2(t)$
₁₈₇ are constant over space and within each set of 200 tracks, but R is random and follows
₁₈₈ a $\Gamma(\mu(t), \sigma^2(t))$ distribution.

₁₈₉ 2) There are no external pressures on the simulated organism. Resources do not deplete,
₁₉₀ and there is no competition nor predator avoidance.

₁₉₁ 3) The organism has a fixed daily energetic requirement that is independent of movement
₁₉₂ rates, and it cannot alter its metabolism or physiology. Additionally, the organism
₁₉₃ does not have energetic reserves, so excess resources cannot be carried over to the next
₁₉₄ track or t .

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

204 Additional information is provided in Appendix B, including the directed acyclical graph
 205 [see fig. B6 and 74] we used to infer causal the mechanisms of changes in H and estimate the
 206 direct effects of $E(R)$ and $\text{Var}(R)$ on H (contrast the graph with fig. C3 and the empirical
 207 case study below).

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

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

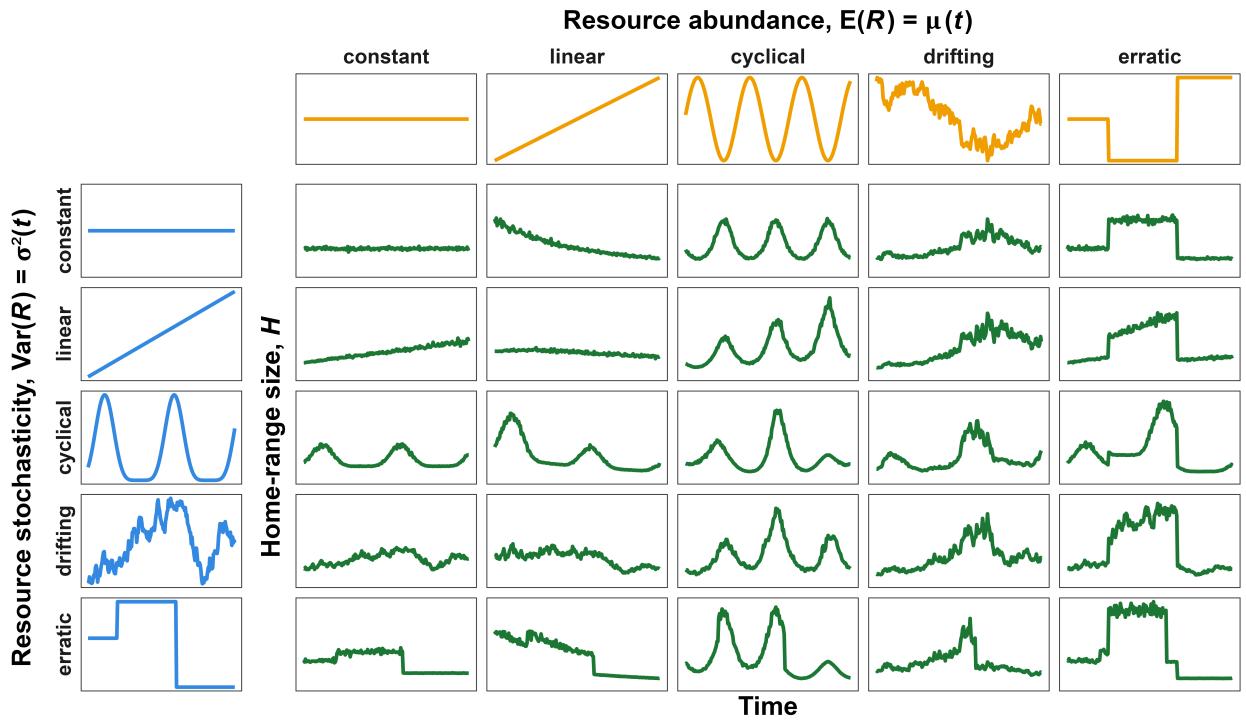


Figure 3: Simulated home-range sizes, H , of an organism living in habitats where the mean and variance in resources are constant, linearly increasing, cyclical, drifting, or erratic over time (but homogenous over space for a given t). Note how H decreases nonlinearly as $\mu(t)$ increases and increases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

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

229 Although the temporal trends in fig. 3 are complex and the effects of $E(R)$ and $\text{Var}(R)$
230 can be hard to disentangle, two simple relationships emerge when H is shown as a function
231 of either $E(R)$ or $\text{Var}(R)$, rather than time (panels A and B of fig. 4). The estimated
232 relationships follow the hypotheses we presented in figs. 1 and 2, although we found that the
233 effect of $\text{Var}(R)$ at average $E(R)$ was linear with a slight sublinear saturation at high values
234 of $\text{Var}(R)$. However, notice that the effect of $\text{Var}(R)$ on $E(H)$ depends strongly on $E(R)$
235 (panel C): When $E(R)$ is low, $E(H)$ is high and $\text{Var}(R)$ does not have a strong effect, but
236 when $E(R)$ is high the effect of $\text{Var}(R)$ on $E(H)$ is exponential. Similarly, $E(H)$ decreases
237 exponentially with $E(R)$ except when $\text{Var}(R)$ is very high.

238 As expected by the changes in the spread of the points in panels A and B of fig. 4, the
239 variance in H , $\text{Var}(H)$, also depends on $E(R)$ and $\text{Var}(R)$ (fig. 4D-F). Since we modeled
240 H using a Gamma family of distributions, we expected $\text{Var}(H)$ to increase with $E(H)$, but
241 the location-scale model removes the assumption of a constant mean-variance relationship
242 (i.e., constant coefficient of variation, $\frac{\mu(t)}{\sigma^2(t)}$). This allowed us to show that the effect of R on
243 $\text{Var}(H)$ is much stronger than the effect of R on $E(H)$. Consequences of these effects are
244 explored in the discussion section.

245 **A case study on a lowland tapir in the Brazilian Cerrado**

246 The simulations in the section above support the hypotheses we presented in the introduction,
247 but they are based on assumptions that are often not met in real natural environments.

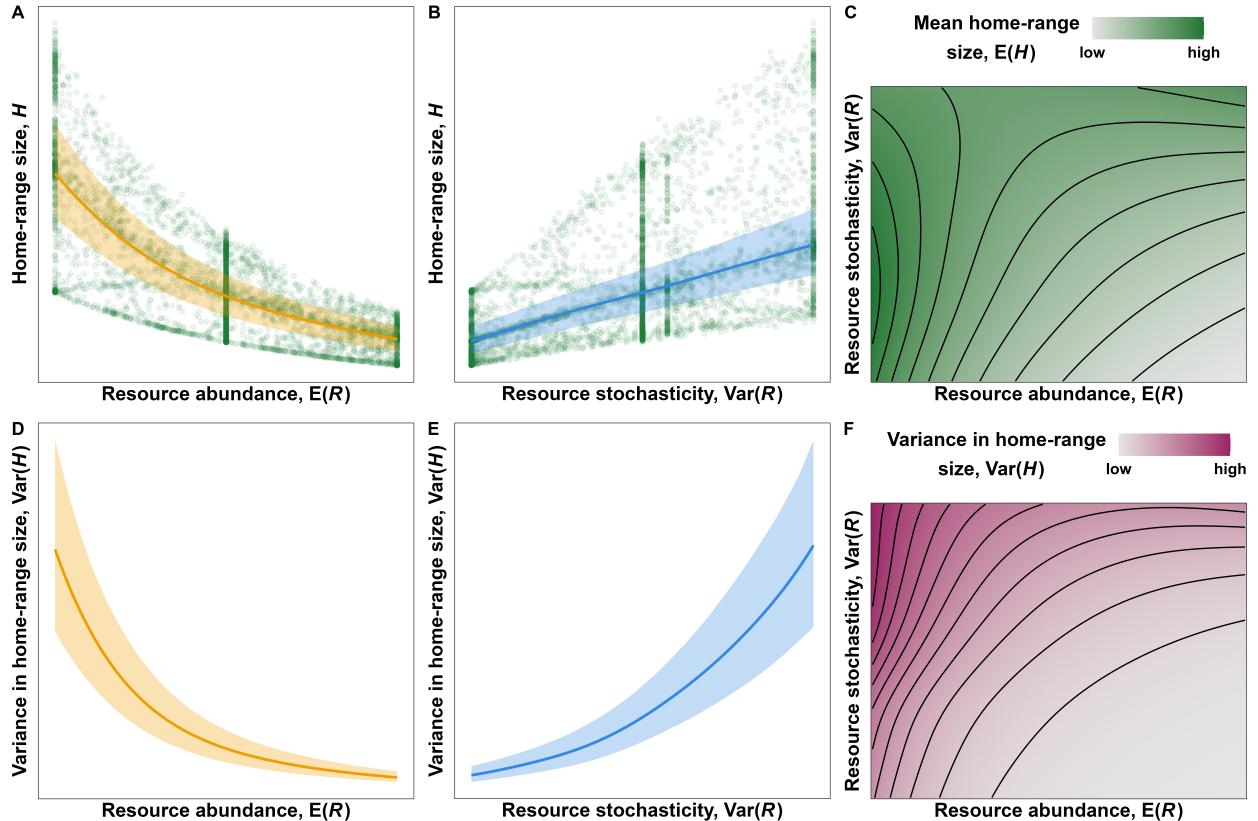


Figure 4: Effects of $E(R)$ and $\text{Var}(R)$ on the mean (A-C) and variance (D-F) in simulated home-range size with 95% Bayesian credible intervals. While the estimated marginal effect of $\text{Var}(R)$ on $E(H)$ is sublinear (panel B), the effect of $\text{Var}(R)$ is superlinear for high values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

248 Organisms live in spatiotemporally heterogeneous and dynamic environments that promote
249 the use of perceptual ranges, navigation, and memory. Together, these abilities result in
250 selective space use that depends on resource availability [11] and resource depletion [12].

251 In this section, we test the hypotheses using empirical tracking data on a lowland tapir
252 from the Brazilian Cerrado along with empirical estimates of $E(R)$ and $\text{Var}(R)$. We measure
253 R using Normalized Difference Vegetation Index [NDVI, see 75], a remote-sensed measure
254 of landscape greenness, as a proxy for forage abundance. Appendix C contains additional
255 information on how we modeled NDVI and the tapir's movement using continuous-time
256 movement models [70,76] and autocorrelated kernel density estimation [77–79].

257 Fig. 5 illustrates how a tapir in the Brazilian Cerrado adapts its 7-day home-range size to
258 spatiotemporal changes in $\mu(t, \vec{u})$ and $\sigma^2(t, \vec{u})$ [telemetry data from the individual labelled as
259 “Anna” in the dataset from 27]. Panels A and B show the changes in seven-day average mean
260 and variance in NDVI, respectively, experienced by the tapir during the tracking period. The
261 mean and variance in NDVI were estimated using a Generalized Additive Model for Location
262 and Scale [GAMLS, 80] with a Beta family of distributions (NDVI values ranged from 0.3534
263 to 0.9475). Panel C shows the changes in the tapir's 7-day home range over time. Note how
264 the tapir uses more space during periods of lower NDVI (e.g., August 2017) and less space
265 during periods with high NDVI (January 2018). Additionally, when resources are scarce
266 and highly unpredictable (August 2018), the tapir uses up to 5 times more space than when
267 resources are abundant and predictable (e.g., January 2018). Finally, panels D and E show
268 the estimated (marginal) effects of $\mu(t, \vec{u})$ and $\sigma^2(t, \vec{u})$ on the tapir's 7-day home-range
269 size. Since $\mu(t, \vec{u})$ and $\sigma^2(t, \vec{u})$ are correlated (panel F) and spatiotemporally autocorrelated
270 (panels A, B, and F), the effects of R on H should be modeled carefully. To avoid over-fitting
271 the model, we constrained the smooth effects of $\mu(t, \vec{u})$ and $\sigma^2(t, \vec{u})$ and their interaction
272 effect to a small basis size ($k = 3$). Additional information is provided in appendix C. The
273 results presented in panels D-F of fig. 5 match our findings from the simulations: The tapir's
274 7-day home range decreases with $\mu(t, \vec{u})$ and 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, $\mu(t, \vec{u})$ and $\sigma^2(t, \vec{u})$ cause the tapir to double her home range (panels D and E), but together they result in an approximate 15-fold change in home-range size (observed range: 0.8 to 12.4 km²; see panel F). Additionally, note how high NDVI values (> 0.8) cause $\sigma^2(t, \vec{u})$ to have little to no effect on home-range size, as indicated by the vertical contour line in panel F.

Discussion

The amount of space organisms use is determined by a multitude of factors [13], but the search for resources is often a main driver of animal how much and where organisms move. This paper builds on earlier theoretical work [15,e.g., 16,17] and presents two hypotheses that describe the effects of resource abundance and stochasticity on organisms' range sizes. We use quantitative simulations and an empirical case study to support the hypotheses and show that, together, they provide 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 we account for in the empirical approach. Below we discuss the strengths and limitations of each approach.

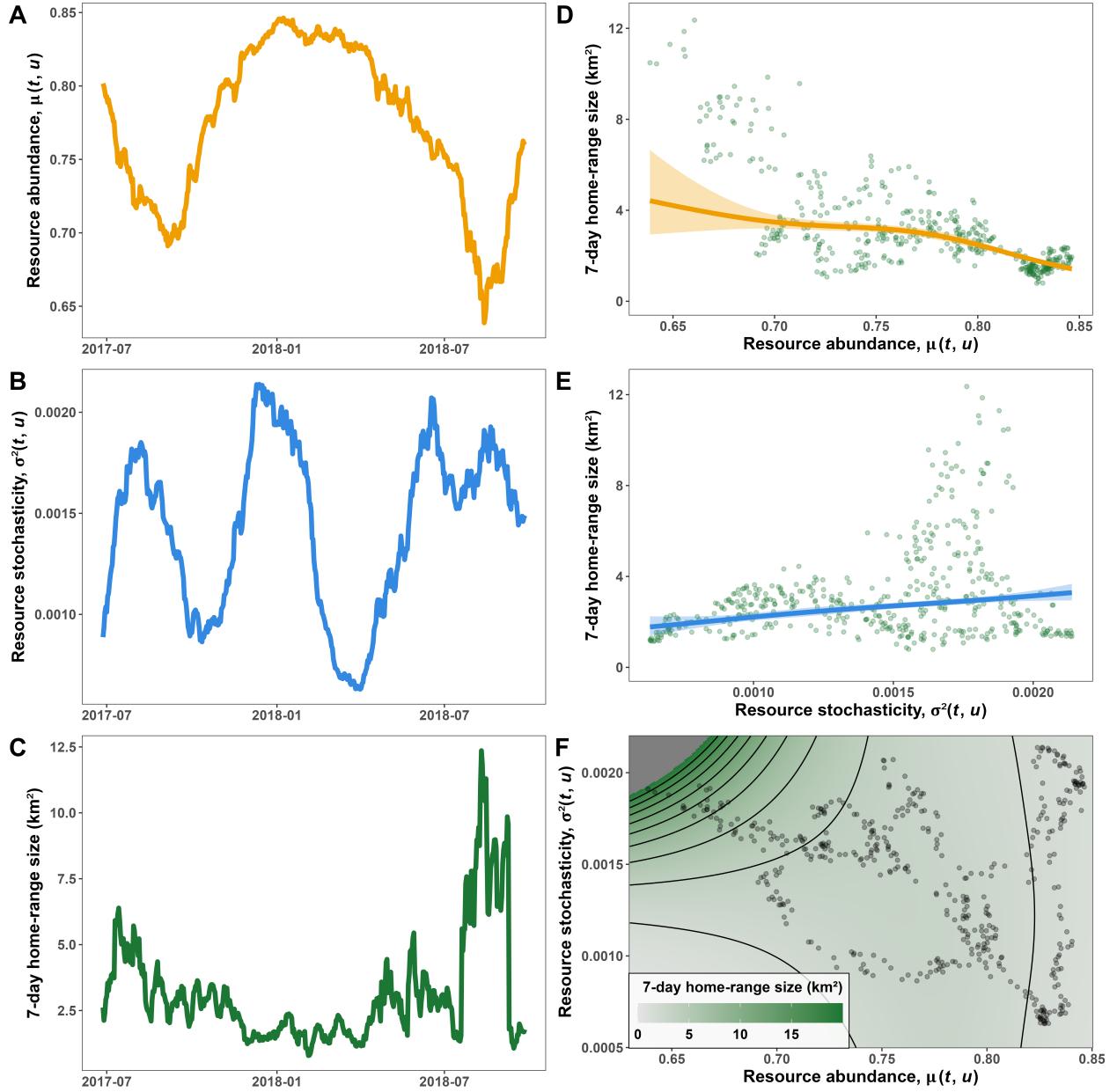


Figure 5: Effects of $\mu(t, \vec{u})$ and $\sigma^2(t, \vec{u})$ on the home-range size of a lowland tapir (*Tapirus terrestris*). (A) Trends in resource abundance over time, $\mu(t, \vec{u})$, estimated as the average mean NDVI at the locations visited by the tapir during a seven-day period. (B) Variance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

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

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

311 Deviations from the simulations offer a means of detecting when the underlying assumptions
312 are inappropriate and how additional factors may affect organisms' responses to changes
313 in $E(R)$ and $\text{Var}(R)$. For example, energetic costs of movement are often non-negligible and
314 depend on organism size [38], movement speed [38], and ambient temperature [1,81]. In addition,
315 an organism may alter its movement behavior, physiology, and energetic needs to buffer
316 itself against changes in $E(R)$ and $\text{Var}(R)$ by using space selectively [67,82–84] and adapting
317 their behavior and physiology over time [15,68]. Before or during periods of scarcity, organisms
318 may cache resources [85], build up fat reserves [43], enter states of dormancy [86–88],
319 or even pause fetal growth [7]. However, organisms may be unable to respond to changes
320 in $E(R)$ and $\text{Var}(R)$ optimally due to various reasons, including limited perceptive range
321 [60], lack of experience [9,45,62–64,89], avoidance of competitors and predators [11,90], or a
322 physiology that is not amenable to things like hibernation or fat storage. Thus organisms
323 may relocate their range to a sub-optimal location [31,32,91,92], which may exacerbate the
324 effects of $E(R)$ and $\text{Var}(R)$ on both mean range size and the variance around it.

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

326 There are two main advantages of taking an empirical approach. Firstly, modeling real-world
327 animal movement data can produce scale-appropriate and easily interpretable estimates.
328 Secondly, empirical models directly quantify the effects of $E(R)$, $\text{Var}(R)$, and confounding
329 variables without having to design complex and time-consuming simulations. However, it
330 is not always possible to quantify confounding variables. For example, while there may be
331 some appropriate proxies of competition, such as density of competitors, these variables may
332 be hard to quantify, and they may not account for the confounding effects appropriately
333 (i.e., the presence of competitors may not reflect competitive pressure). This is problematic
334 if one is interested in estimating the direct causal effect of $E(R)$ and $\text{Var}(R)$, which requires
335 removing any non-negligible confounding effects [74].

336 Similarly, if R is often non-measurable. Proxies of R , such as NDVI [75], which may
337 introduce complexities. While R and NDVI are correlated for many species [43,44,89,e.g.,
338 93,94,95], the relationship between the two can be weak [96], satellite-dependent [97], and
339 nonlinear [97,98]. This complexity can introduce two sources of bias: ecosystem-level biases
340 (indicated as Z in the directed acyclical graph in fig. C3) and satellite-level confounding
341 variables (S in fig. C3). Examples of ecosystem-level biases are the effects of competition,
342 predation, habitat connectivity, and movement costs, all of which can depend on habitat
343 quality, and, consequently, be correlated nonlinearly to R and NDVI [33,99]. Resource-rich
344 patches can attract larger amounts of competitors [11] and predators [18], which may, in
345 turn, increase pressures from competition and predation [12,37]. However, such pressures
346 may result in both an expansion of the range [33,99] or a contraction, since larger ranges can
347 be harder to defend and result in higher movement costs [33,100] and encounter rates [101].
348 Satellite-level confounds include information loss due to coarse spatiotemporal resolution
349 [97,98], satellite-level error [97,98,102], and other limitations of remote sensing (e.g., inability
350 to quantify specific resources or small-scale resource depletion). However, nonlinear models
351 such as Generalized Additive Models [103] can help account for preferences for intermediate

352 values of remotely-sensed R [e.g., young grass rather than mature grasslands, see 97].

353 Conclusion

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

359 Recent advances in computational power have greatly increased analysts' ability to fit
360 computationally demanding models [104,105] that allow biologists to move beyond only
361 considering changes in mean conditions. By accounting for changes in stochasticity, we can
362 start developing a more comprehensive understanding of how organisms adapt to the dynamic
363 environments organisms live in, including recent changes in climate [106] and increases in
364 the frequency and intensity of extreme events [65,66,107–109].

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³⁷⁵ **Code and data availability**

³⁷⁶ All code and data used for this manuscript is available on GitHub at <https://github.com/>
³⁷⁷ QuantitativeEcologyLab/hr-resource-stoch, with the exception of the tapir data, which is
³⁷⁸ available at <https://github.com/StefanoMezzini/tapirs>.

³⁷⁹ **Conflict of interest**

³⁸⁰ The authors declare there are no conflicts of interest.

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