

How resource abundance and stochasticity affect organisms' range sizes

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¹ Abstract

² **Background:** The amount of space organisms use is thought to be tightly linked to the
³ availability of resources within their habitats, such that organisms living in productive habi-
⁴ tats generally require less space than those in resource-poor habitats. This hypothesis has
⁵ widespread empirical support, but existing studies have focused primarily on responses to
⁶ the mean amount of resources, while responses to the variance around the mean are still
⁷ largely unknown. Since organisms adjust to variable environmental conditions, failing to
⁸ consider the effects of resource (un)predictability can result in an insufficient understand-
⁹ ing of an organism's range size, which results in challenges for both ecological theory and
¹⁰ applied conservation. **Methods:** We leverage the available literature to provide a unify-
¹¹ ing framework and two hypotheses for the effects of resource abundance and stochasticity
¹² on range sizes. We then use simulated movement data using continuous-time movement
¹³ models to demonstrate how the combined effects of mean and variance in resources inter-
¹⁴ act to shape predictable patterns in range size. Finally, we test the two hypotheses using
¹⁵ real-world tracking data on a lowland tapir (*Tapirus terrestris*) from the Brazilian Cerrado.
¹⁶ **Results:** Organisms' range sizes decrease nonlinearly with resource abundance and increase
¹⁷ nonlinearly with resource stochasticity. Additionally, the effects of resource stochasticity
¹⁸ depend strongly on resource abundance, and organisms' responses to resource abundance
¹⁹ and stochasticity can be complex, since the distribution and predictability of resources can
²⁰ exacerbate the effects of other drivers of movement, such as resource depletion, competition,
²¹ and predation. **Conclusions:** Accounting for resource abundance and stochasticity is cru-
²² cial for understanding the movement behavior of free-ranging organisms. Failing to account
²³ for resource stochasticity can lead to an incomplete and incorrect understanding of how and
²⁴ why organisms move, particularly during periods of rapid change.

²⁵ **Background**

²⁶ The amount of resources an organism is able to access is a strong determinant of its odds
²⁷ of survival and reproduction. Resource limitations can cause individuals to experience a
²⁸ negative energetic balance, which can then result in lower fitness [1,2], altered physiology
²⁹ [2–5], lower chance of reproduction [2,6–8], and even death [9,10]. Thus, many organisms
³⁰ adapt their behaviors and/or physiology in response to changes in local resource abundance
³¹ to ensure their needs are met.

³² While there are many ways that individuals can respond to resource availability, move-
³³ ment represents one of the most readily available traits that species can adjust [11–13]. The
³⁴ relationship between organisms' movement and resource abundance has long been of interest
³⁵ to biologists. In his seminal paper, Burt [14] considered the search for food as the primary
³⁶ driver for movement within an organism's home range. Three decades after, Southwood [15]
³⁷ suggested that change in resource abundance drives how organisms decide where to live and
³⁸ when to reproduce. Two years later, Harestad and Bunnel [16] proposed that the simplest
³⁹ relationship between resource abundance and an organism's home-range size is

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

⁴⁰ where H is the organism's home-range size, C is the organism's resource consumption rate
⁴¹ (kcal day^{-1}), and R is the resources the organism can access ($\text{kcal day}^{-1} \text{ unit area}^{-1}$).
⁴² Harestad and Bunnel's model is simple to conceptualize, and it allows for testable predictions,
⁴³ but few studies are structured around a set of theoretical expectations such as Harestad
⁴⁴ and Bunnel's hypothesis. Many researchers have since demonstrated that organisms adapt
⁴⁵ their range sizes in response to resources abundance, but results are typically reported as
⁴⁶ independent, novel findings. Perhaps more problematic is the fact that, while much work
⁴⁷ has been done on estimating organisms' responses to mean resource abundance, there is
⁴⁸ little information on how organisms respond to variance around the mean [i.e., resource

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

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

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

⁷⁵ **Resources as a random variable**

⁷⁶ Resources are often unpredictable (and difficult to quantify), since they depend on various
⁷⁷ factors which cannot be accounted for easily, including climate [7,28,29], weather [29,30],
⁷⁸ competitive pressure [31,32], and differences in energetics at among individuals [7] and species
⁷⁹ [33]. Thus, we can treat the amount of resources R at a given point in time (t) and space
⁸⁰ (location vector \vec{u}) as a random variable, denoted as $R(t, \vec{u})$. Treating resources as a random
⁸¹ variable allows us to leverage techniques from probability theory and statistics, such as the
⁸² expectation of a random variable (i.e., its mean) and its variance around the mean. We
⁸³ indicate the expected value and variance of random variable R using $E(R)$ and $\text{Var}(R)$,
⁸⁴ respectively, and we use $\mu(t, \vec{u})$ and $\sigma^2(t, \vec{u})$ to indicate them as functions of time (t) and
⁸⁵ space (\vec{u}). Appendix A defines and expands on the concepts of probability distributions,
⁸⁶ expected value, variance, and provides examples of them for 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 [34–
⁹¹ 36]. As the abundance of essential resources fluctuates, motile organisms can move to new
⁹² locations or 'patches' to meet their requirements [12,37], but they must also account for costs
⁹³ of movement [38].

⁹⁴ Fig. 1 illustrates our first of two hypotheses, which is similar to that presented by [16].
⁹⁵ When $E(R)$ is high, we expect organisms' ranges to be relatively small and near the smallest
⁹⁶ amount of space required to survive [25,26,e.g., 39]. Like Harestad and Bunnel [16], we also
⁹⁷ expect organisms' range sizes to increase nonlinearly as $E(R)$ decreases, but we highlight
⁹⁸ that organisms may adopt different behaviors at low values of $E(R)$. These behaviors include
⁹⁹ maximal home range expansion [31,home range size is limited by vagility, habitat structure,

competition, and predation, e.g., 32,40,41], migration [42–44], and nomadism [21,23,45,46]. 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: 47, moose, *Alces alces*: 21, eagles, *Haliaeetus leucocephalus*: 22,48, lesser flamingos, *Phoeniconaias minor*: 49]. Still, switches from range residency to nomadism (or vice-versa) will occur over evolutionary timescales rather than over an organism's lifespan (Fig. 1), since larger ranges require greater vagility, which, in turn, is facilitated by the development of morphological features such as hinged joints and elongated limbs [33,50–52].

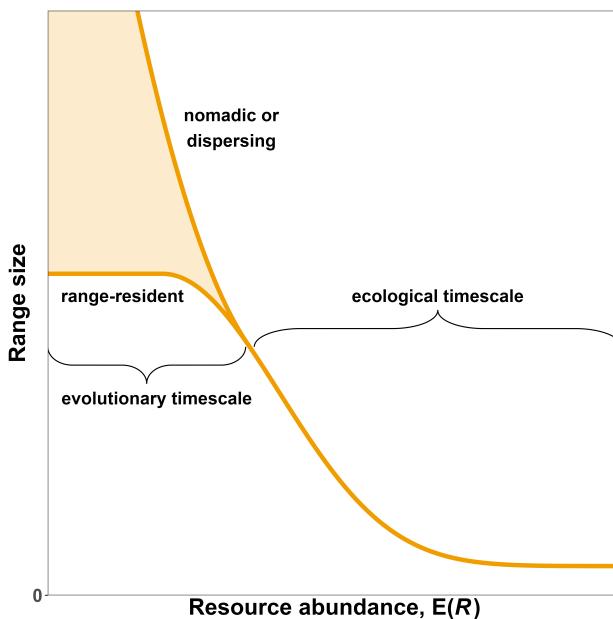


Figure 1: Hypothesized range size of an organism as a function of resource abundance, $E(R)$. We expect low values of $E(R)$ to result in a large range, since organisms are forced to explore large areas to collect the resources they require to survive, whether they be range-resident, nomadic, or migratory.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

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 [19, e.g., 39,53–55]. 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

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

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

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

126 Recognizing changes in $\text{Var}(R)$ helps account for the residual, fine-scale variation in R
127 after accounting for trends in the large-scale average R [e.g., variations in plant phenology
128 between years after accounting for mean seasonal trends, see 59]. However, when both
129 $E(R)$ and $\text{Var}(R)$ change over time (fig. A2), disentangling changes in $E(R)$ and $\text{Var}(R)$ is
130 not simple [60]. Statistically, this confound occurs because the more change one attributes
131 to $\mu(t, \vec{u})$ (i.e., the wigglier it is), the smaller $\sigma^2(t, \vec{u})$ becomes. Conversely, the smoother
132 $\mu(t, \vec{u})$ is, the larger $\sigma^2(t, \vec{u})$ becomes. Biologically, it is important because an organism's
133 perception scale determines whether it attributes a change in R to a trend in $E(R)$ or as
134 a stochastic event [i.e., due to $\text{Var}(R)$; see [59]]. An organism's perception of changes in
135 R will also depend strongly on the its cognitive capacities and memory [9,61–64]. Whether
136 an organism is able to predict trends in $\sigma^2(t, \vec{u})$ or not, environmental variability is thought
137 to reduce a landscape's energetic balance [24], which, in turn, decreases organisms' fitness
138 [e.g., 10] and increases their range size. While this behavioral response occurs with both
139 predictable and unpredictable stochasticity, extreme and rare events are more likely to have

¹⁴⁰ a stronger effect due to their unpredictability and magnitude [65,66]. A few recent studies
¹⁴¹ support these hypotheses [20,24,29,46,67], but many of them are limited in geographic and
¹⁴² taxonomic scales or fail to account for nonlinear relationships, so the extent to which these
¹⁴³ preliminary findings can be generalized is currently unknown. Thus, there remains a need
¹⁴⁴ for developing a more complete understanding of how organisms' range sizes changes with
¹⁴⁵ environmental stochasticity.

¹⁴⁶ Similarly to $E(R)$, we hypothesize $\text{Var}(R)$ has a nonlinear effect on an organism's range
¹⁴⁷ size. When $\text{Var}(R)$ is low enough that R is relatively predictable, we expect organisms to be
¹⁴⁸ range-resident with small home ranges, and we do not expect small changes in $\text{Var}(R)$ to have
¹⁴⁹ a noticeable effect. As resources become increasingly unpredictable, we expect home range
¹⁵⁰ size to increase progressively faster (fig. 2) because: (1) as $\text{Var}(R)$ increases, the chances of
¹⁵¹ finding low R increase superlinearly, (2) the added movement required to search for food
¹⁵² increases organisms' energetic requirements, and (3) stochasticity reduces an organism's abil-
¹⁵³ ity to specialize and reduce competition for R [68]. If resources remain highly unpredictable
¹⁵⁴ over long periods of time (e.g., multiple lifespans), organisms may evolve or develop new
¹⁵⁵ and consistent behaviors (e.g., nomadism) or adaptations (e.g., increased fat storage or food
¹⁵⁶ caching) to buffer themselves against times of unpredictably low R . Conversely, if changes
¹⁵⁷ in $\sigma^2(t, \vec{u})$ are sufficiently predictable, organisms may learn to anticipate and prepare for
¹⁵⁸ times of greater stochasticity by pre-emptively caching food, reducing energetic needs,
¹⁵⁹ migrating, or relying on alternative food sources [e.g., 69].

¹⁶⁰ Interactive effects of $E(R)$ and $\text{Var}(R)$

¹⁶¹ We have provided the case for why both $E(R)$ and $\text{Var}(R)$ should be expected to affect
¹⁶² organisms' range size, but we presented the two parameters as independent drivers of move-
¹⁶³ ment. However, organisms may respond to changes in $\sigma^2(t, \vec{u})$ more when resources are
¹⁶⁴ scarce than when they are abundant. Consequently, an organism's movement behavior is
¹⁶⁵ likely to be a function of not only the marginal effects of $E(R)$ and $\text{Var}(R)$ but also their

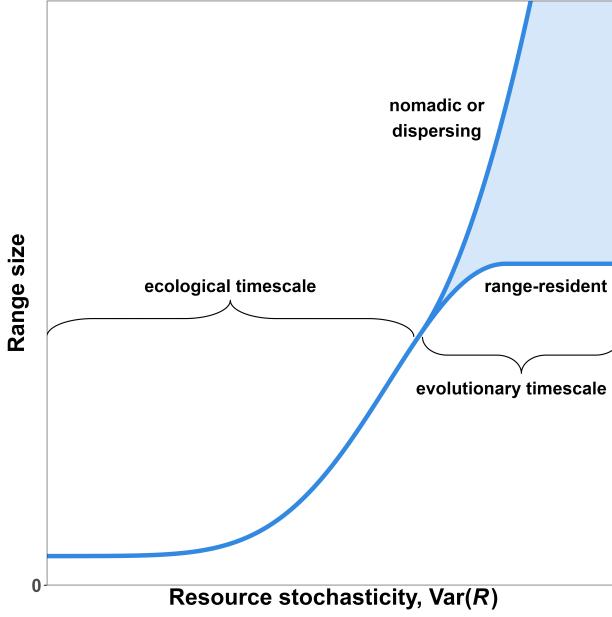


Figure 2: Hypothesized range size of an organism as a function of resource stochasticity, $\text{Var}(R)$. We expect low values of $\text{Var}(R)$ to result in small home-ranges, since organisms are able to depend on relatively predictable resources. As $\text{Var}(R)$ increases, range size should increase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

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

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

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

179 be interpreted as purely exploratory or memoryless movement.

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

181 Each time the simulated individual moved to a new cell, it collected R resources sampled
182 from a Gamma distribution. The mean and variance of the distribution were defined by a
183 series of deterministic functions $\mu(t)$ and $\sigma^2(t)$ (orange and blue lines in fig. 3). The value
184 of t was constant within each set of 200 tracks, so the distribution R was sampled from
185 was independent of both the organism's location and its time spent moving. Tracks were
186 truncated once the organism reached satiety, and the organism was given enough time to
187 return to $\langle 0, 0 \rangle$ independently from the following track (section 2.1 of Appendix B). Finally,
188 we fit an OUF movement model [73] to the set of tracks to calculate the 95% Gaussian
189 home-range size using the formula

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

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

191 We designed the simulations to estimate the effects of $E(R)$ and $\text{Var}(R)$ in simplistic
192 environments where organisms could only respond by searching for longer periods of time.

193 Consequently, we made the following assumptions:

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

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

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

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

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

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

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

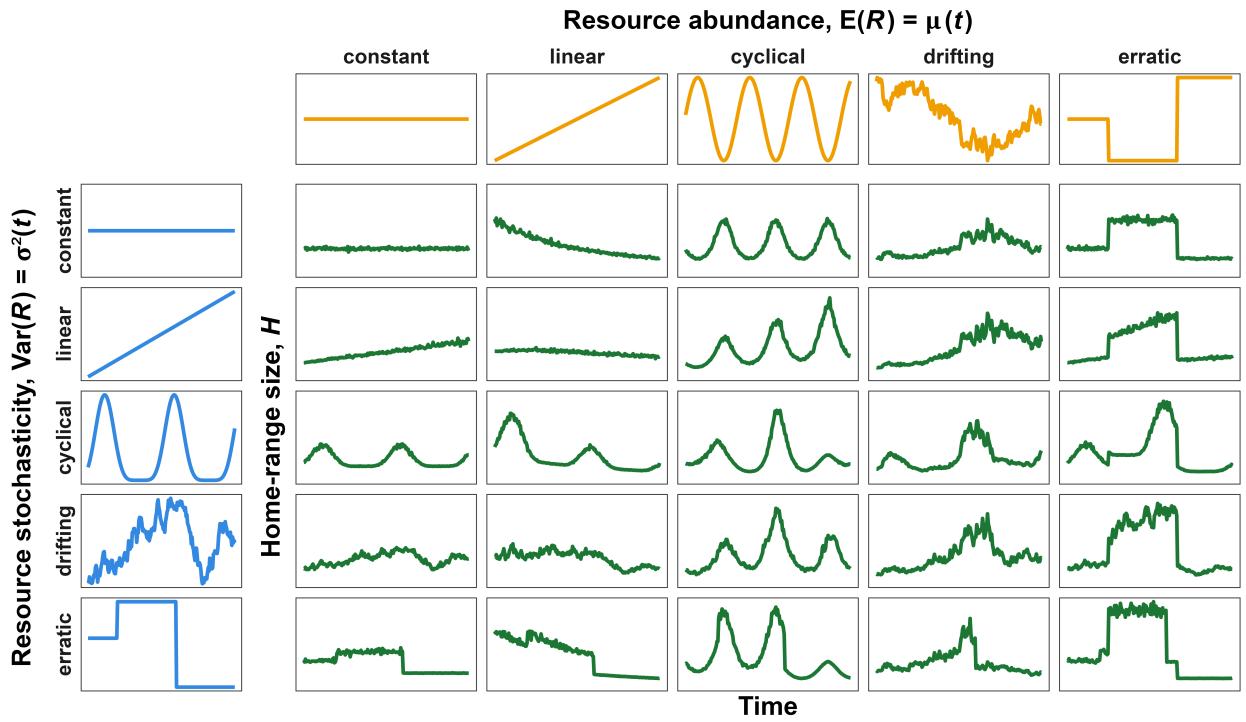


Figure 3: Simulated home-range sizes, H , of an organism living in habitats where the mean and variance in resources are constant, linearly increasing, cyclical, drifting, or erratic over time (but homogeneous over space for a given t). Note how H decreases nonlinearly as $\mu(t)$ increases and increases 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 The remaining panels in fig. 3 illustrate how $E(R)$ and $\text{Var}(R)$ jointly affect H and how
231 confusing the effects can be. Since $E(R)$ and $\text{Var}(R)$ have opposite effects on H , disentangling
232 the effects can be particularly difficult when both parameters change in a correlated manner
233 (e.g., linear $E(R)$ and $\text{Var}(R)$). When both $E(R)$ and $\text{Var}(R)$ increase linearly, H initially
234 increases since the effect of $\text{Var}(R)$ is stronger, but then decreases as the effect of $E(R)$ begins
235 to dominate. Difficulties in disentangling the two effects are explored in greater depth in the
236 case study in the following section.

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

246 As expected by the changes in the spread of the points in panels A and B of fig. 4, the
247 variance in H , $\text{Var}(H)$, also depends on $E(R)$ and $\text{Var}(R)$ (fig. 4D-F). Since we modeled
248 H using a Gamma family of distributions, we expected $\text{Var}(H)$ to increase with $E(H)$, but
249 the location-scale model removes the assumption of a constant mean-variance relationship
250 (i.e., constant coefficient of variation, $\frac{\mu(t)}{\sigma^2(t)}$). This allowed us to show that the effect of R on
251 $\text{Var}(H)$ is much stronger than the effect of R on $E(H)$. Consequences of these effects are
252 explored in the discussion section.

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

254 The simulations in the section above support the hypotheses we presented in the background
255 section, but they are based on assumptions that are often not met in real natural environ-

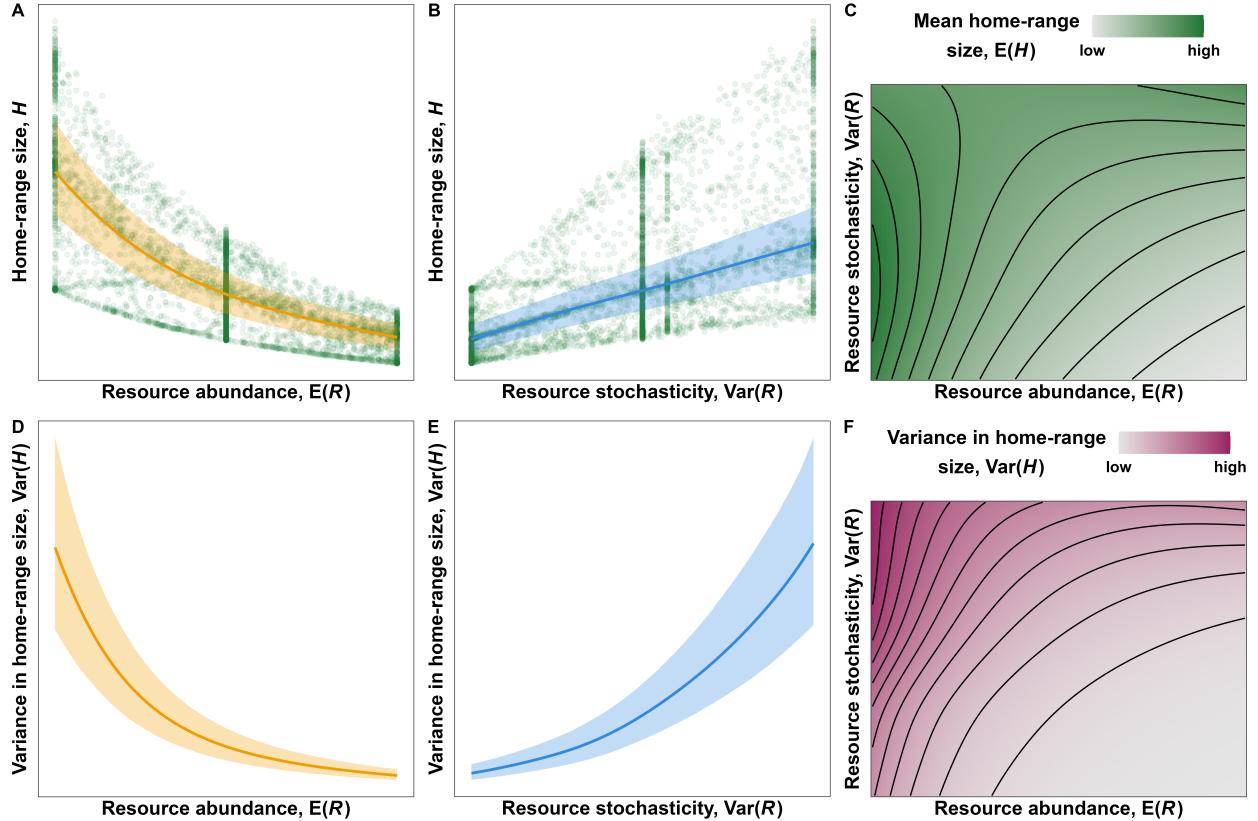


Figure 4: Effects of $E(R)$ and $\text{Var}(R)$ on the mean (A-C) and variance (D-F) in simulated home-range size with 95% Bayesian credible intervals. While the estimated marginal effect of $\text{Var}(R)$ on $E(H)$ is sublinear (panel B), the effect of $\text{Var}(R)$ is superlinear for high values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

256 ments. Organisms live in spatiotemporally heterogeneous and dynamic environments that
257 promote the use of perceptual ranges, navigation, and memory. Together, these abilities
258 result in selective space use that depends on resource availability [11] and resource depletion
259 [12].

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

266 Fig. 5 illustrates how a tapir in the Brazilian Cerrado adapts its 7-day home-range
267 size to spatiotemporal changes in estimated $\mu(t, \vec{u})$ and $\sigma^2(t, \vec{u})$ (telemetry data from the
268 individual labelled as “Anna” in the dataset from [27]). Panels A and B show the changes in
269 seven-day average mean and variance in NDVI, respectively, experienced by the tapir during
270 the tracking period. The mean and variance in NDVI were estimated using a Generalized
271 Additive Model for Location and Scale [GAMLS, 80] with a Beta family of distributions
272 (NDVI values ranged from 0.3534 to 0.9475). Panel C shows the changes in the tapir’s
273 7-day home range over time. Note how the tapir uses more space during periods of lower
274 NDVI (e.g., August 2017) and less space during periods with high NDVI (January 2018).
275 Additionally, when resources are scarce and highly unpredictable (August 2018), the tapir
276 uses up to 5 times more space than when resources are abundant and predictable (e.g.,
277 January 2018). Finally, panels D and E show the estimated (marginal) effects of $\hat{\mu}(t, \vec{u})$ and
278 $\hat{\sigma}^2(t, \vec{u})$ 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
279 F) and spatiotemporally autocorrelated (panels A, B, and F), the effects of R on H should
280 be modeled carefully. To avoid over-fitting the model, we constrained the smooth effects
281 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
282 information is provided in appendix C. The results presented in panels D-F of fig. 5 match

283 our findings from the simulations: The tapir's 7-day home range decreases with $\hat{\mu}(t, \vec{u})$ and
284 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,
285 $\hat{\mu}(t, \vec{u})$ and $\hat{\sigma}^2(t, \vec{u})$ cause the tapir to double her home range (panels D and E), but together
286 they result in an approximate 15-fold change in home-range size (observed range: 0.8 to 12.4
287 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
288 have little to no effect on home-range size, as indicated by the vertical contour line in panel
289 F.

290 Discussion

291 The amount of space organisms use is determined by a multitude of factors [13], but the
292 search for resources is often a main driver of animal how much and where organisms move.
293 This paper builds on earlier theoretical work [15,e.g., 16,17] and presents two hypotheses
294 that describe the effects of resource abundance and stochasticity on organisms' range sizes.
295 We use quantitative simulations and an empirical case study to support the hypotheses
296 and show that, together, they provide a simple framework for understanding how motile
297 organisms adapt their movement in dynamic environments. Separately, resource abundance
298 and stochasticity have simple but opposing effects on organisms' range sizes: H decreases
299 with $E(R)$ and increases with $\text{Var}(R)$. Together, the degree to which $E(R)$ affects H depends
300 on $\text{Var}(R)$, and vice-versa, so organisms' responses to resource dynamics can be complex.
301 The simulated and empirical results suggest qualitatively similar marginal effects of $E(R)$
302 and $\text{Var}(R)$, but there are differences in the estimated interactive effects. In the simulated
303 data, $\text{Var}(R)$ has little effect when $E(R)$ is low and a strong effect when $E(R)$ is high, while
304 the opposite is true for the empirical data. This difference is due to two reasons. Firstly, the
305 shape and symmetry of bounded distributions such as Gamma ($R > 0$) and Beta ($0 < R < 1$)
306 distributions depend on both $E(R)$ and $\text{Var}(R)$ (figs. A3, A4), but $\text{Var}(R)$ does not affect
307 the shape of a Gamma distribution as much if $E(R)$ is low (fig. B3). Secondly, and perhaps
308 more interestingly, the simulation approach does not account for real-world adaptations to

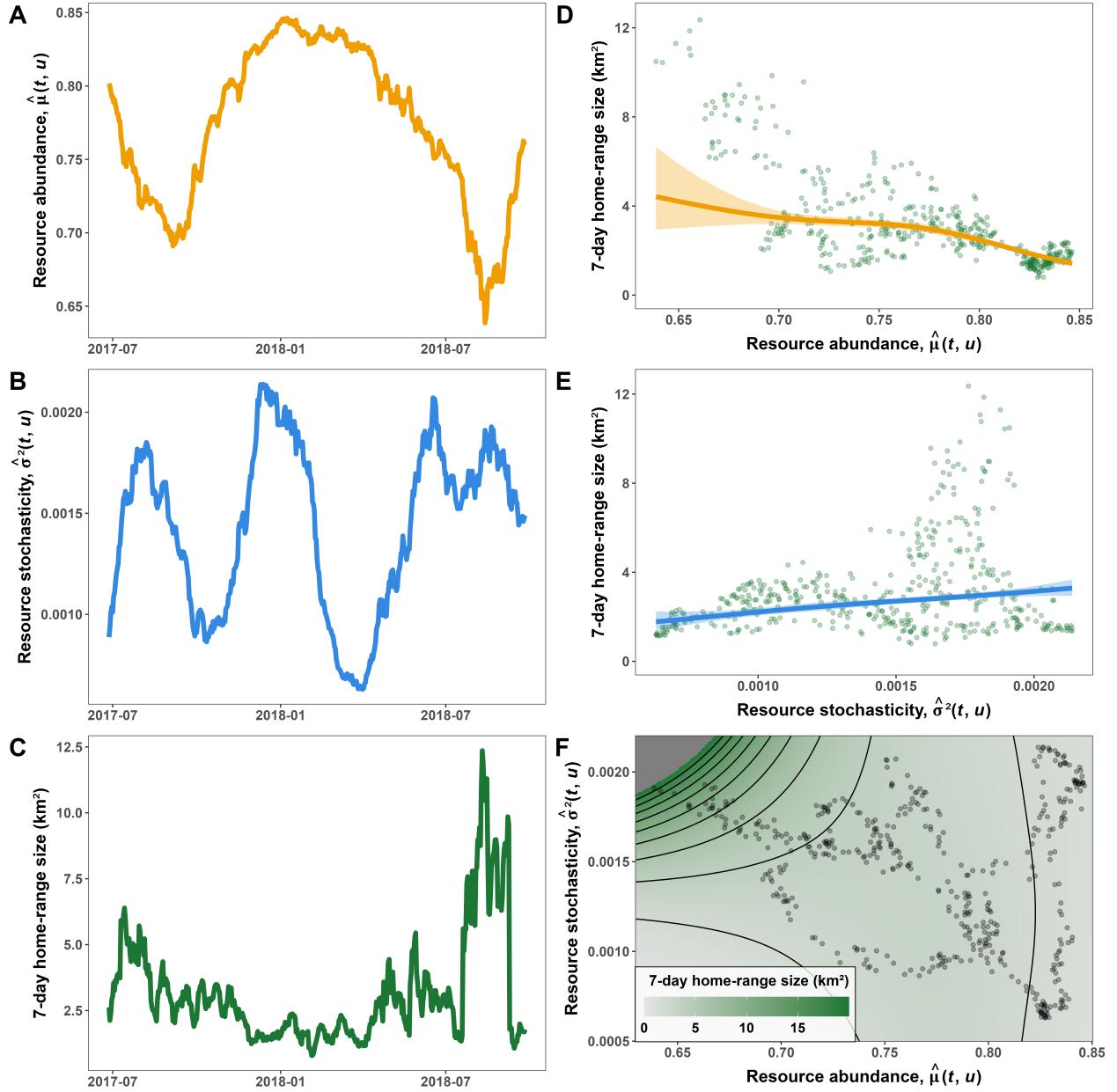


Figure 5: Effects of estimated $\mu(t, \bar{u})$ and $\sigma^2(t, \bar{u})$ on the home-range size of a lowland tapir (*Tapirus terrestris*). (A) Trends in resource abundance over time, $\hat{\mu}(t, \bar{u})$, estimated as the average mean NDVI at the locations visited by the tapir during a seven-day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

- 309 $E(R)$ and $\text{Var}(R)$ such as selective space use, which we account for in the empirical approach.
310 Below we discuss the strengths and limitations of each approach.

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

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

321 Deviations from the simulations offer a means of detecting when the underlying assump-
322 tions are inappropriate and how additional factors may affect organisms' responses to changes
323 in $E(R)$ and $\text{Var}(R)$. For example, energetic costs of movement are often non-negligible and
324 depend on organism size [38], movement speed [38], and ambient temperature [1,81]. In addi-
325 tion, an organism may alter its movement behavior, physiology, and energetic needs to buffer
326 itself against changes in $E(R)$ and $\text{Var}(R)$ by using space selectively [67,82–84] and adapting
327 their behavior and physiology over time [15,68]. Before or during periods of scarcity, organ-
328 isms may cache resources [85], build up fat reserves [43], enter states of dormancy [86–88],
329 or even pause fetal growth [7]. However, organisms may be unable to respond to changes
330 in $E(R)$ and $\text{Var}(R)$ optimally due to various reasons, including limited perceptive range
331 [60], lack of experience [9,45,62–64,89], avoidance of competitors and predators [11,90], or a
332 physiology that is not amenable to things like hibernation or fat storage. Thus, organisms
333 may relocate their range to a sub-optimal location [31,32,91,92], which may exacerbate the
334 effects of $E(R)$ and $\text{Var}(R)$ on both mean range size and the variance around it.

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

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

346 Similarly, if R is often non-measurable. Proxies of R , such as NDVI [75], which may
347 introduce complexities. While R and NDVI are correlated for many species [43,44,89,e.g.,
348 93,94,95], the relationship between the two can be weak [96], satellite-dependent [97], and
349 nonlinear [97,98]. This complexity can introduce two sources of bias: ecosystem-level biases
350 (indicated as Z in the directed acyclical graph in fig. C3) and satellite-level confounding
351 variables (S in fig. C3). Examples of ecosystem-level biases are the effects of competition,
352 predation, habitat connectivity, and movement costs, all of which can depend on habitat
353 quality, and, consequently, be correlated nonlinearly to R and NDVI [33,99]. Resource-rich
354 patches can attract larger amounts of competitors [11] and predators [18], which may, in
355 turn, increase pressures from competition and predation [12,37]. However, such pressures
356 may result in both an expansion of the range [33,99] or a contraction, since larger ranges can
357 be harder to defend and result in higher movement costs [33,100] and encounter rates [101].
358 Satellite-level confounds include information loss due to coarse spatiotemporal resolution
359 [97,98], satellite-level error [97,98,102], and other limitations of remote sensing (e.g., inability
360 to quantify specific resources or small-scale resource depletion). However, nonlinear models
361 such as Generalized Additive Models [103] can help account for preferences for intermediate

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

363 **Conclusions**

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

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

³⁷⁵ **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
³⁷⁶ $\mu(t)$	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

³⁷⁷ **Declarations**

³⁷⁸ **Ethics approval and consent to participate**

³⁷⁹ Not applicable.

³⁸⁰ **Consent for publication**

³⁸¹ Not applicable.

382 **Availability of data and materials**

383 All code and data used for this manuscript is available on GitHub at <https://github.com/>
384 QuantitativeEcologyLab/hr-resource-stoch, with the exception of two simulated datasets
385 that were greater than 100 MB and the tapir data. The simulated data can be produced
386 by running the scripts in the repository, while the tapir data is available at <https://github.com/StefanoMezzini/tapirs>.
387

388 **Competing interests**

389 The authors declare that they have no competing interests.

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395 **Authors' contributions**

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

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⁴¹⁴ **References**

- ⁴¹⁵ 1. Hou R, Chapman CA, Jay O, Guo S, Li B, Raubenheimer D. Cold and hungry: Combined
⁴¹⁶ effects of low temperature and resource scarcity on an edge-of-range temperate primate,
⁴¹⁷ the golden snub-nose monkey. *Ecography* [Internet]. 2020 [cited 2022 Oct 3];43:1672–82.
⁴¹⁸ Available from: <https://onlinelibrary.wiley.com/doi/10.1111/ecog.05295>
- ⁴¹⁹ 2. Le Bot T, Lescroël A, Fort J, Péron C, Gimenez O, Provost P, et al. Fishery discards
⁴²⁰ do not compensate natural prey shortage in northern gannets from the english channel.
⁴²¹ *Biological Conservation* [Internet]. 2019 [cited 2022 Oct 3];236:375–84. Available from:
⁴²² <https://linkinghub.elsevier.com/retrieve/pii/S0006320718310930>
- ⁴²³ 3. Dai Pra R, Mohr SM, Merriman DK, Bagriantsev SN, Gracheva EO. Ground squir-
⁴²⁴rels initiate sexual maturation during hibernation. *Current Biology* [Internet]. 2022 [cited
⁴²⁵ 2022 Sep 2];32:1822–1828.e4. Available from: <https://linkinghub.elsevier.com/retrieve/pii/>
⁴²⁶ S0960982222002548
- ⁴²⁷ 4. Rocha JL, Godinho R, Brito JC, Nielsen R. Life in deserts: The genetic basis of
⁴²⁸ mammalian desert adaptation. *Trends in Ecology & Evolution* [Internet]. 2021 [cited
⁴²⁹ 2022 Sep 2];36:637–50. Available from: <https://linkinghub.elsevier.com/retrieve/pii/>
⁴³⁰ S0169534721000744
- ⁴³¹ 5. Wessling EG, Deschner T, Mundry R, Pruetz JD, Wittig RM, Kühl HS. Seasonal varia-
⁴³²tion in physiology challenges the notion of chimpanzees (*pan troglodytes verus*) as a forest-
⁴³³adapted species. *Front Ecol Evol* [Internet]. 2018 [cited 2022 Sep 2];6:60. Available from:
⁴³⁴ <http://journal.frontiersin.org/article/10.3389/fevo.2018.00060/full>

- 435 6. Stefanescu C, Ubach A, Wiklund C. Timing of mating, reproductive status and resource
436 availability in relation to migration in the painted lady butterfly. *Animal Behaviour* [Internet].
437 2021 [cited 2022 Sep 2];172:145–53. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S0003347220303742>
- 439 7. Schmidt NM, Grøndahl C, Evans AL, Desforges J-P, Blake J, Hansen LH, et al. On the in-
440 terplay between hypothermia and reproduction in a high arctic ungulate. *Sci Rep* [Internet].
441 2020 [cited 2022 Sep 2];10:1514. Available from: <http://www.nature.com/articles/s41598-020-58298-8>
- 443 8. Douglas DJT, Pearce-Higgins JW. Relative importance of prey abundance and habitat
444 structure as drivers of shorebird breeding success and abundance: Drivers of shorebird breed-
445 ing success and abundance. *Anim Conserv* [Internet]. 2014 [cited 2022 Nov 8];17:535–43.
446 Available from: <https://onlinelibrary.wiley.com/doi/10.1111/acv.12119>
- 447 9. Foley C, Pettorelli N, Foley L. Severe drought and calf survival in elephants. *Bi-
448 ology Letters* [Internet]. 2008 [cited 2020 Feb 12];4:541–4. Available from: <https://royalsocietypublishing.org/doi/10.1098/rsbl.2008.0370>
- 450 10. Berger J, Hartway C, Gruzdev A, Johnson M. Climate degradation and extreme icing
451 events constrain life in cold-adapted mammals. *Scientific Reports* [Internet]. 2018 [cited
452 2020 Jan 24];8:1156. Available from: <http://www.nature.com/articles/s41598-018-19416-9>
- 453 11. Kacelnik A, Krebs JR, Bernstein C. The ideal free distribution and predator-prey popu-
454 lations. *Trends in Ecology & Evolution* [Internet]. 1992 [cited 2024 Jan 31];7:50–5. Available
455 from: <https://linkinghub.elsevier.com/retrieve/pii/016953479290106L>

- 456 12. Charnov EL. Optimal foraging, the marginal value theorem. *Theoretical Population*
457 *Biology* [Internet]. 1976 [cited 2024 Jan 31];9:129–36. Available from: <https://linkinghub.elsevier.com/retrieve/pii/004058097690040X>
- 459 13. Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, et al. A movement
460 ecology paradigm for unifying organismal movement research. *Proc Natl Acad Sci USA*
461 [Internet]. 2008 [cited 2022 Mar 9];105:19052–9. Available from: <https://pnas.org/doi/full/10.1073/pnas.0800375105>
- 463 14. Burt WH. Territoriality and home range concepts as applied to mammals. *Journal of*
464 *Mammalogy* [Internet]. 1943 [cited 2022 Jan 31];24:346. Available from: <https://academic.oup.com/jmammal/article-lookup/doi/10.2307/1374834>
- 466 15. Southwood TRE. Habitat, the templet for ecological strategies? *The Journal of Animal*
467 *Ecology* [Internet]. 1977 [cited 2022 Feb 4];46:336. Available from: <https://www.jstor.org/stable/3817?origin=crossref>
- 469 16. Harestad AS, Bunnel FL. Home range and body weight—a reevaluation. *Ecology* [In-
470 ternet]. 1979 [cited 2022 Sep 5];60:389–402. Available from: <http://doi.wiley.com/10.2307/1937667>
- 472 17. Stephens DW, Charnov EL. Optimal foraging: Some simple stochastic models. *Behav*
473 *Ecol Sociobiol* [Internet]. 1982 [cited 2024 Jan 31];10:251–63. Available from: <http://link.springer.com/10.1007/BF00302814>
- 475 18. Duncan C, Nilssen EB, Linnell JDC, Pettorelli N. Life-history attributes and resource
476 dynamics determine intraspecific home-range sizes in carnivora. *Remote Sens Ecol Con-*

- ⁴⁷⁷ serv [Internet]. 2015 [cited 2024 May 29];1:39–50. Available from: <https://zslpublications.onlinelibrary.wiley.com/doi/10.1002/rse2.6>
- ⁴⁷⁹ 19. Rizzuto M, Leroux SJ, Vander Wal E, Richmond IC, Heckford TR, Balluffi-Fry J, et al.
- ⁴⁸⁰ Forage stoichiometry predicts the home range size of a small terrestrial herbivore. *Oecologia*
- ⁴⁸¹ [Internet]. 2021 [cited 2022 Mar 2];197:327–38. Available from: <https://link.springer.com/10.1007/s00442-021-04965-0>
- ⁴⁸³ 20. Broekman MJE, Hilbers JP, Hoeks S, Huijbregts MAJ, Schipper AM, Tucker MA. Envi-
- ⁴⁸⁴ ronmental drivers of global variation in home range size of terrestrial and marine mammals.
- ⁴⁸⁵ *Journal of Animal Ecology* [Internet]. 2024 [cited 2024 Jul 29];93:488–500. Available from:
- ⁴⁸⁶ <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2656.14073>
- ⁴⁸⁷ 21. Singh NJ, Börger L, Dettki H, Bunnefeld N, Ericsson G. From migration to nomadism:
- ⁴⁸⁸ Movement variability in a northern ungulate across its latitudinal range. *Ecological Appli-*
- ⁴⁸⁹ *cations* [Internet]. 2012 [cited 2022 Nov 17];22:2007–20. Available from: <http://doi.wiley.com/10.1890/12-0245.1>
- ⁴⁹¹ 22. Wheat RE, Lewis SB, Wang Y, Levi T, Wilmers CC. To migrate, stay put, or wander?
- ⁴⁹² Varied movement strategies in bald eagles (*haliaeetus leucocephalus*). *Mov Ecol* [Internet].
- ⁴⁹³ 2017 [cited 2022 Oct 17];5:9. Available from: <http://movementecologyjournal.biomedcentral.com/articles/10.1186/s40462-017-0102-4>
- ⁴⁹⁵ 23. Teitelbaum CS, Mueller T. Beyond migration: Causes and consequences of nomadic ani-
- ⁴⁹⁶ mal movements. *Trends in Ecology & Evolution* [Internet]. 2019 [cited 2022 Feb 1];34:569–81.
- ⁴⁹⁷ Available from: <https://linkinghub.elsevier.com/retrieve/pii/S0169534719300527>

- 498 24. Chevin L-M, Lande R, Mace GM. Adaptation, plasticity, and extinction in a changing
499 environment: Towards a predictive theory. Kingsolver JG, editor. PLoS Biology [Internet].
500 2010 [cited 2020 Nov 11];8:e1000357. Available from: <https://dx.plos.org/10.1371/journal.pbio.1000357>
- 502 25. Herfindal I, Linnell JDC, Odden J, Nilsen EB, Andersen R. Prey density, environmental
503 productivity and home-range size in the eurasian lynx (*lynx lynx*). Journal of Zoology
504 [Internet]. 2005 [cited 2022 Sep 23];265:63–71. Available from: <https://onlinelibrary.wiley.com/doi/10.1017/S0952836904006053>
- 506 26. Nilsen EB, Herfindal I, Linnell JDC. Can intra-specific variation in carnivore home-range
507 size be explained using remote-sensing estimates of environmental productivity? Écoscience
508 [Internet]. 2005 [cited 2021 Nov 29];12:68–75. Available from: <https://www.tandfonline.com/doi/full/10.2980/i1195-6860-12-1-68.1>
- 510 27. Medici EP, Mezzini S, Fleming CH, Calabrese JM, Noonan MJ. Movement ecology
511 of vulnerable lowland tapirs between areas of varying human disturbance. Mov Ecol [In-
512 ternet]. 2022 [cited 2022 Mar 14];10:14. Available from: <https://movementecologyjournal.biomedcentral.com/articles/10.1186/s40462-022-00313-w>
- 514 28. Lindstedt SL, Boyce MS. Seasonality, fasting endurance, and body size in mammals.
515 The American Naturalist [Internet]. 1985 [cited 2022 Feb 4];125:873–8. Available from:
516 <https://www.journals.uchicago.edu/doi/10.1086/284385>
- 517 29. Morellet N, Bonenfant C, Börger L, Ossi F, Cagnacci F, Heurich M, et al. Seasonality,
518 weather and climate affect home range size in roe deer across a wide latitudinal gradient
519 within europe. Coulson T, editor. Journal of Animal Ecology [Internet]. 2013 [cited 2020

⁵²⁰ Nov 11];82:1326–39. Available from: <http://doi.wiley.com/10.1111/1365-2656.12105>

⁵²¹ 30. Fjelldal MA, Wright J, Stawski C. Nightly torpor use in response to weather conditions
⁵²² and individual state in an insectivorous bat. *Oecologia* [Internet]. 2021 [cited 2022 Oct
⁵²³ 3];197:129–42. Available from: <https://link.springer.com/10.1007/s00442-021-05022-6>

⁵²⁴ 31. Tórrez-Herrera LL, Davis GH, Crofoot MC. Do monkeys avoid areas of home range
⁵²⁵ overlap because they are dangerous? A test of the risk hypothesis in white-faced capuchin
⁵²⁶ monkeys (*cebus capucinus*). *Int J Primatol* [Internet]. 2020 [cited 2022 Mar 9];41:246–64.
⁵²⁷ Available from: <http://link.springer.com/10.1007/s10764-019-00110-0>

⁵²⁸ 32. Rich LN, Mitchell MS, Gude JA, Sime CA. Anthropogenic mortality, intraspecific com-
⁵²⁹ petition, and prey availability influence territory sizes of wolves in montana. *J Mammal*
⁵³⁰ [Internet]. 2012 [cited 2022 Mar 10];93:722–31. Available from: <https://academic.oup.com/jmammal/article-lookup/doi/10.1093/jmammal/93.4.722>

⁵³² 33. Jetz W, Carbone C, Fulford J, Brown JH. The scaling of animal space use. *Science*
⁵³³ [Internet]. 2004 [cited 2022 Mar 3];306:266–8. Available from: <https://www.science.org/doi/10.1126/science.1102138>

⁵³⁵ 34. Harvey PH, Clutton-Brock TH. Primate home-range size and metabolic needs. *Behav*
⁵³⁶ *Ecol Sociobiol* [Internet]. 1981 [cited 2022 Nov 12];8:151–5. Available from: <http://link.springer.com/10.1007/BF00300828>

⁵³⁸ 35. Baldwin R, Bywater A. Nutritional energetics of animals. *Annual review of nutrition*.
⁵³⁹ 1984;4:101–14.

540 36. Reich PB. Body size, geometry, longevity and metabolism: Do plant leaves behave like
541 animal bodies? Trends in Ecology & Evolution [Internet]. 2001 [cited 2022 Oct 17];16:674–
542 80. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S0169534701023060>

543 37. Brown JS, Laundre JW, Gurung M. The ecology of fear: Optimal foraging, game
544 theory, and trophic interactions. Journal of Mammalogy [Internet]. 1999 [cited 2024 Jan
545 31];80:385–99. Available from: <https://academic.oup.com/jmammal/article-lookup/doi/10.2307/1383287>

547 38. Taylor CR, Heglund NC, Maloiy GM. Energetics and mechanics of terrestrial locomotion.
548 I. Metabolic energy consumption as a function of speed and body size in birds and mammals.
549 Journal of Experimental Biology [Internet]. 1982 [cited 2022 Dec 12];97:1–21. Available
550 from: <https://journals.biologists.com/jeb/article/97/1/1/34642/Energetics-and-mechanics-of-terrestrial-locomotion>

552 39. Relyea RA, Lawrence RK, Demarais S. Home range of desert mule deer: Testing the
553 body-size and habitat-productivity hypotheses. The Journal of Wildlife Management [In-
554 ternet]. 2000 [cited 2021 Nov 29];64:146. Available from: <https://www.jstor.org/stable/3802984?origin=crossref>

556 40. Dawe KL, Bayne EM, Boutin S. Influence of climate and human land use on the dis-
557 tribution of white-tailed deer (*odocoileus virginianus*) in the western boreal forest. Cana-
558 dian Journal of Zoology [Internet]. 2014 [cited 2020 Oct 23];92:353–63. Available from:
559 <http://www.nrcresearchpress.com/doi/10.1139/cjz-2013-0262>

560 41. Berger-Tal O, Saltz D. Invisible barriers: Anthropogenic impacts on inter- and
561 intra-specific interactions as drivers of landscape-independent fragmentation. Phil

- 562 Trans R Soc B [Internet]. 2019 [cited 2022 Aug 11];374:20180049. Available from:
563 <https://royalsocietypublishing.org/doi/10.1098/rstb.2018.0049>
- 564 42. Samarra FIP, Tavares SB, Béesau J, Deecke VB, Fennell A, Miller PJO, et al. Movements
565 and site fidelity of killer whales (*orcinus orca*) relative to seasonal and long-term shifts in
566 herring (*clupea harengus*) distribution. Mar Biol [Internet]. 2017 [cited 2022 Nov 7];164:159.
567 Available from: <http://link.springer.com/10.1007/s00227-017-3187-9>
- 568 43. Middleton AD, Merkle JA, McWhirter DE, Cook JG, Cook RC, White PJ, et al. Green-
569 wave surfing increases fat gain in a migratory ungulate. Oikos [Internet]. 2018 [cited 2022
570 Sep 2];127:1060–8. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/oik.05227>
- 571 44. Geremia C, Merkle JA, Eacker DR, Wallen RL, White PJ, Hebblewhite M, et al. Mi-
572 grating bison engineer the green wave. Proc Natl Acad Sci USA [Internet]. 2019 [cited
573 2022 Mar 2];116:25707–13. Available from: <http://www.pnas.org/lookup/doi/10.1073/pnas.1913783116>
- 575 45. Polansky L, Kilian W, Wittemyer G. Elucidating the significance of spatial memory
576 on movement decisions by african savannah elephants using state-space models. Proc
577 R Soc B [Internet]. 2015 [cited 2022 Feb 10];282:20143042. Available from: <https://royalsocietypublishing.org/doi/10.1098/rspb.2014.3042>
- 579 46. Nandintsetseg D, Bracis C, Leimgruber P, Kaczensky P, Buuveibaatar B, Lkhagvasuren
580 B, et al. Variability in nomadism: Environmental gradients modulate the movement behav-
581 iors of dryland ungulates. Ecosphere [Internet]. 2019 [cited 2020 Nov 11];10. Available from:
582 <https://onlinelibrary.wiley.com/doi/abs/10.1002/ecs2.2924>

- 583 47. Teitelbaum CS, Fagan WF, Fleming CH, Dressler G, Calabrese JM, Leimgruber P, et
584 al. How far to go? Determinants of migration distance in land mammals. Festa-Bianchet
585 M, editor. *Ecol Lett* [Internet]. 2015 [cited 2022 Sep 23];18:545–52. Available from: <https://doi.org/10.1111/ele.12435>
- 587 48. Poessel SA, Woodbridge B, Smith BW, Murphy RK, Bedrosian BE, Bell DA, et al.
588 Interpreting long-distance movements of non-migratory golden eagles: Prospecting and
589 nomadism? *Ecosphere* [Internet]. 2022 [cited 2022 Nov 18];13. Available from: <https://doi.org/10.1002/ecs2.4072>
- 591 49. Pretorius MD, Leeuwner L, Tate GJ, Botha A, Michael MD, Durgaprasad K, et al.
592 Movement patterns of lesser flamingos *phoeniconaias minor* : Nomadism or partial migra-
593 tion? *Wildlife Biology* [Internet]. 2020 [cited 2022 Nov 17];2020:1–11. Available from:
594 <https://doi.org/10.2981/wlb.00728>
- 595 50. Hirt MR, Jetz W, Rall BC, Brose U. A general scaling law reveals why the largest
596 animals are not the fastest. *Nat Ecol Evol* [Internet]. 2017 [cited 2022 Mar 11];1:1116–22.
597 Available from: [http://www.nature.com/articles/s41559-017-0241-4](https://doi.org/10.1038/s41559-017-0241-4)
- 598 51. Andersson K. Elbow-joint morphology as a guide to forearm function and foraging
599 behaviour in mammalian carnivores. *Zoological Journal of the Linnean Society* [Internet].
600 2004 [cited 2023 Jul 6];142:91–104. Available from: <https://doi.org/10.1111/j.1096-3642.2004.00129.x>
- 602 52. Samuels JX, Meachen JA, Sakai SA. Postcranial morphology and the locomotor habits
603 of living and extinct carnivorans. *J Morphol* [Internet]. 2013 [cited 2023 Jul 6];274:121–46.
604 Available from: <https://doi.org/10.1002/jmor.20077>

- 605 53. Bista D, Baxter GS, Hudson NJ, Lama ST, Murray PJ. Effect of disturbances and
606 habitat fragmentation on an arboreal habitat specialist mammal using GPS telemetry: A
607 case of the red panda. *Landsc Ecol* [Internet]. 2022 [cited 2022 Aug 24];37:795–809. Available
608 from: <https://link.springer.com/10.1007/s10980-021-01357-w>
- 609 54. Bradsworth N, White JG, Rendall AR, Carter N, Whisson DA, Cooke R. Using thresh-
610 olds to determine priorities for apex predator conservation in an urban landscape. *Land-
611 scape and Urban Planning* [Internet]. 2022 [cited 2022 Oct 18];228:104559. Available from:
612 <https://github.com/ropensci/MODISstsp>
- 613 55. McClintic LF, Taylor JD, Jones JC, Singleton RD, Wang G. Effects of spatiotemporal
614 resource heterogeneity on home range size of american beaver. *J Zool* [Internet]. 2014 [cited
615 2022 Nov 12];293:134–41. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/jzo.12128>
- 617 56. Lucherini M, Lovari S. Habitat richness affects home range size in the red fox *vulpes
618 vulpes*. *Behavioural Processes* [Internet]. 1996 [cited 2021 Nov 29];36:103–5. Available from:
619 <https://linkinghub.elsevier.com/retrieve/pii/0376635795000186>
- 620 57. Simcharoen A, Savini T, Gale GA, Simcharoen S, Duangchantrasiri S, Pakpien S, et
621 al. Female tiger *panthera tigris* home range size and prey abundance: Important metrics
622 for management. *Oryx* [Internet]. 2014 [cited 2022 Nov 8];48:370–7. Available from: https://www.cambridge.org/core/product/identifier/S0030605312001408/type/journal_article
- 624 58. Watson J. Ferruginous hawk (*buteo regalis*) home range and resource use on northern
625 grasslands in canada. 2020 [cited 2022 Nov 8]; Available from: <http://rgdoi.net/10.13140/RG.2.2.32404.32648>

- 627 59. Levin SA. The problem of pattern and scale in ecology: The robert h. MacArthur
628 award lecture. *Ecology* [Internet]. 1992 [cited 2024 Jan 31];73:1943–67. Available from:
629 <https://esajournals.onlinelibrary.wiley.com/doi/10.2307/1941447>
- 630 60. Steixner-Kumar S, Gläscher J. Strategies for navigating a dynamic world. *Science*
631 [Internet]. 2020 [cited 2022 Mar 9];369:1056–7. Available from: <https://www.science.org/doi/10.1126/science.abd7258>
- 633 61. Mueller T, O'Hara RB, Converse SJ, Urbanek RP, Fagan WF. Social learning of mi-
634 gratory performance. *Science* [Internet]. 2013 [cited 2022 Nov 24];341:999–1002. Available
635 from: <https://www.science.org/doi/10.1126/science.1237139>
- 636 62. Abrahms B, Hazen EL, Aikens EO, Savoca MS, Goldbogen JA, Bograd SJ, et al. Memory
637 and resource tracking drive blue whale migrations. *Proc Natl Acad Sci USA* [Internet]. 2019
638 [cited 2022 Mar 3];116:5582–7. Available from: <http://www.pnas.org/lookup/doi/10.1073/pnas.1819031116>
- 640 63. Falcón-Cortés A, Boyer D, Merrill E, Frair JL, Morales JM. Hierarchical, memory-based
641 movement models for translocated elk (*cervus canadensis*). *Front Ecol Evol* [Internet]. 2021
642 [cited 2022 Feb 4];9:702925. Available from: <https://www.frontiersin.org/articles/10.3389/fevo.2021.702925/full>
- 644 64. Fagan WF, Lewis MA, Auger-Méthé M, Avgar T, Benhamou S, Breed G, et al. Spatial
645 memory and animal movement. Clobert J, editor. *Ecol Lett* [Internet]. 2013 [cited 2022
646 Mar 9];16:1316–29. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/ele.12165>
- 647 65. Logares R, Nuñez M. Black swans in ecology and evolution: The importance of improba-

648 ble but highly influential events. Ideas in Ecology and Evolution [Internet]. 2012 [cited 2020
649 Feb 12]; Available from: <https://ojs.library.queensu.ca/index.php/IEE/article/view/4311>

650 66. Anderson SC, Branch TA, Cooper AB, Dulvy NK. Black-swan events in animal
651 populations. Proceedings of the National Academy of Sciences [Internet]. 2017 [cited
652 2020 Jan 24];114:3252–7. Available from: <http://www.pnas.org/lookup/doi/10.1073/pnas.1611525114>

654 67. Riotte-Lambert L, Matthiopoulos J. Environmental predictability as a cause and
655 consequence of animal movement. Trends in Ecology & Evolution [Internet]. 2020 [cited
656 2020 Nov 11];35:163–74. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S0169534719302885>

658 68. Levins RA. Evolution in changing environments: Some theoretical explorations. 3.
659 printing. Princeton, NJ: Princeton Univ. Press; 1974.

660 69. Van Baalen M, Křivan V, Van Rijn PCJ, Sabelis MW. Alternative food, switching
661 predators, and the persistence of predator-prey systems. The American Naturalist [Internet].
662 2001 [cited 2024 May 20];157:512–24. Available from: <https://www.journals.uchicago.edu/doi/10.1086/319933>

664 70. Fleming CH, Calabrese JM. Ctmm: Continuous-time movement modeling [Internet].
665 2021. Available from: <https://github.com/ctmm-initiative/ctmm>, <https://groups.google.com/g/ctmm-user>

667 71. R Core Team. R: A language and environment for statistical computing [Internet].
668 Vienna, Austria: R Foundation for Statistical Computing; 2023. Available from: <https://>

669 //www.R-project.org/

670 72. Gurarie E, Fleming CH, Fagan WF, Laidre KL, Hernández-Piiego J, Ovaskainen O.
671 Correlated velocity models as a fundamental unit of animal movement: Synthesis and
672 applications. *Mov Ecol* [Internet]. 2017 [cited 2023 Sep 6];5:13. Available from: <http://movementecologyjournal.biomedcentral.com/articles/10.1186/s40462-017-0103-3>

674 73. Fleming CH, Calabrese JM, Mueller T, Olson KA, Leimgruber P, Fagan WF. From
675 fine-scale foraging to home ranges: A semivariance approach to identifying movement modes
676 across spatiotemporal scales. *The American Naturalist* [Internet]. 2014 [cited 2022 Jul
677 26];183:E154–67. Available from: <https://www.journals.uchicago.edu/doi/10.1086/675504>

678 74. McElreath R. Statistical rethinking: A bayesian course with examples in r and stan.
679 Boca Raton: CRC Press/Taylor & Francis Group; 2016.

680 75. Pettorelli N, Ryan S, Mueller T, Bunnefeld N, Jedrzejewska B, Lima M, et al. The
681 normalized difference vegetation index (NDVI): Unforeseen successes in animal ecology. *Clim
682 Res* [Internet]. 2011 [cited 2022 Mar 8];46:15–27. Available from: <http://www.int-res.com/abstracts/cr/v46/n1/p15-27/>

684 76. Noonan MJ, Fleming CH, Akre TS, Drescher-Lehman J, Gurarie E, Harrison
685 A-L, et al. Scale-insensitive estimation of speed and distance traveled from animal
686 tracking data. *Mov Ecol* [Internet]. 2019 [cited 2021 Jun 23];7:35. Available from:
687 <https://movementecologyjournal.biomedcentral.com/articles/10.1186/s40462-019-0177-1>

688 77. Noonan MJ, Tucker MA, Fleming CH, Akre TS, Alberts SC, Ali AH, et al. A comprehen-
689 sive analysis of autocorrelation and bias in home range estimation. *Ecological Monographs*

- 690 [Internet]. 2019 [cited 2020 Oct 23];89:e01344. Available from: <https://onlinelibrary.wiley.com/doi/abs/10.1002/ecm.1344>
- 691
- 692 78. Alston JM, Fleming CH, Kays R, Streicher JP, Downs CT, Ramesh T, et al. Mitigating pseudoreplication and bias in resource selection functions with autocorrelation-informed
693 weighting. *Methods Ecol Evol* [Internet]. 2022 [cited 2022 Dec 12];2041–210X.14025. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/2041-210X.14025>
- 694
- 695
- 696 79. Silva I, Fleming CH, Noonan MJ, Alston J, Folta C, Fagan WF, et al. Autocorrelation-informed home range estimation: A review and practical guide. *Methods Ecol Evol*
697 [Internet]. 2022 [cited 2022 Jul 26];13:534–44. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/2041-210X.13786>
- 698
- 699
- 700 80. Wood SN, Pya N, Säfken B. Smoothing parameter and model selection for general
701 smooth models. *Journal of the American Statistical Association* [Internet]. 2016 [cited
702 2020 Apr 3];111:1548–63. Available from: <https://www.tandfonline.com/doi/full/10.1080/01621459.2016.1180986>
- 703
- 704 81. Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. Toward a metabolic theory
705 of ecology. *Ecology* [Internet]. 2004 [cited 2022 Mar 3];85:1771–89. Available from: <http://doi.wiley.com/10.1890/03-9000>
- 706
- 707 82. Johnson DH. The comparison of usage and availability measurements for evaluating
708 resource preference. *Ecology* [Internet]. 1980 [cited 2024 May 17];61:65–71. Available from:
709 <https://esajournals.onlinelibrary.wiley.com/doi/10.2307/1937156>
- 710 83. Rickbeil GJM, Merkle JA, Anderson G, Atwood MP, Beckmann JP, Cole EK, et

⁷¹¹ al. Plasticity in elk migration timing is a response to changing environmental conditions.
⁷¹² Glob Change Biol [Internet]. 2019 [cited 2022 Jan 20];25:2368–81. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/gcb.14629>

⁷¹⁴ 84. Ranc N, Cagnacci F, Moorcroft PR. Memory drives the formation of animal home ranges:
⁷¹⁵ Evidence from a reintroduction. Coulson T, editor. Ecology Letters [Internet]. 2022 [cited
⁷¹⁶ 2022 Nov 16];25:716–28. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/ele.13869>

⁷¹⁸ 85. Nespolo RF, Mejias C, Bozinovic F. Why bears hibernate? Redefining the scaling
⁷¹⁹ energetics of hibernation. Proc R Soc B [Internet]. 2022 [cited 2022 Nov 21];289:20220456.
⁷²⁰ Available from: <https://royalsocietypublishing.org/doi/10.1098/rspb.2022.0456>

⁷²¹ 86. Goldberg AR, Conway CJ. Hibernation behavior of a federally threatened ground
⁷²² squirrel: Climate change and habitat selection implications. Hayes L, editor. Journal
⁷²³ of Mammalogy [Internet]. 2021 [cited 2022 Nov 21];102:574–87. Available from: <https://academic.oup.com/jmammal/article/102/2/574/6224539>

⁷²⁵ 87. Reher S, Ehlers J, Rabarison H, Dausmann KH. Short and hyperthermic torpor responses
⁷²⁶ in the malagasy bat *macronycteris commersoni* reveal a broader hypometabolic scope in
⁷²⁷ heterotherms. J Comp Physiol B [Internet]. 2018 [cited 2022 Oct 3];188:1015–27. Available
⁷²⁸ from: <http://link.springer.com/10.1007/s00360-018-1171-4>

⁷²⁹ 88. Mohr SM, Bagriantsev SN, Gracheva EO. Cellular, molecular, and physiological adap-
⁷³⁰ tations of hibernation: The solution to environmental challenges. Annu Rev Cell Dev Biol
⁷³¹ [Internet]. 2020 [cited 2022 Oct 3];36:315–38. Available from: <https://www.annualreviews.org/doi/10.1146/annurev-cellbio-012820-095945>

- 733 89. Merkle JA, Sawyer H, Monteith KL, Dwinnell SPH, Fralick GL, Kauffman MJ. Spatial
734 memory shapes migration and its benefits: Evidence from a large herbivore. Gaillard J,
735 editor. *Ecol Lett* [Internet]. 2019 [cited 2022 Sep 5];22:1797–805. Available from: <https://doi.org/10.1111/ele.13362>
- 737 90. Fretwell SD, Lucas HL. On territorial behavior and other factors influencing habitat
738 distribution in birds: I. Theoretical development. *Acta Biotheor* [Internet]. 1969 [cited 2024
739 Apr 8];19:16–36. Available from: <http://link.springer.com/10.1007/BF01601953>
- 740 91. Ciuti S, Northrup JM, Muhly TB, Simi S, Musiani M, Pitt JA, et al. Effects of humans
741 on behaviour of wildlife exceed those of natural predators in a landscape of fear. Moreira
742 N, editor. *PLoS ONE* [Internet]. 2012 [cited 2022 Aug 11];7:e50611. Available from: <https://doi.org/10.1371/journal.pone.0050611>
- 744 92. Burson A, Stomp M, Greenwell E, Grosse J, Huisman J. Competition for nutrients
745 and light: Testing advances in resource competition with a natural phytoplankton com-
746 munity. *Ecology* [Internet]. 2018 [cited 2022 Sep 2];99:1108–18. Available from: <https://doi.org/10.1002/ecy.2187>
- 748 93. Phillips LB, Hansen AJ, Flather CH. Evaluating the species energy relationship with the
749 newest measures of ecosystem energy: NDVI versus MODIS primary production. *Remote
750 Sensing of Environment* [Internet]. 2008 [cited 2024 Feb 14];112:4381–92. Available from:
751 <https://linkinghub.elsevier.com/retrieve/pii/S0034425708002460>
- 752 94. Seigle-Ferrand J, Atmeh K, Gaillard J-M, Ronget V, Morellet N, Garel M, et al. A
753 systematic review of within-population variation in the size of home range across ungulates:
754 What do we know after 50 years of telemetry studies? *Front Ecol Evol* [Internet]. 2021 [cited

⁷⁵⁵ 2022 Aug 16];8:555429. Available from: <https://www.frontiersin.org/articles/10.3389/fevo.2020.555429/full>

⁷⁵⁷ 95. Merkle JA, Monteith KL, Aikens EO, Hayes MM, Hersey KR, Middleton AD, et al.
⁷⁵⁸ Large herbivores surf waves of green-up during spring. Proc R Soc B [Internet]. 2016 [cited
⁷⁵⁹ 2024 Feb 14];283:20160456. Available from: <https://royalsocietypublishing.org/doi/10.1098/rspb.2016.0456>

⁷⁶¹ 96. Gautam H, Arulmalar E, Kulkarni MR, Vidya TNC. NDVI is not reliable as a surrogate
⁷⁶² of forage abundance for a large herbivore in tropical forest habitat. Biotropica [Internet].
⁷⁶³ 2019 [cited 2024 Feb 14];51:443–56. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/btp.12651>

⁷⁶⁵ 97. Huang S, Tang L, Hupy JP, Wang Y, Shao G. A commentary review on the use of
⁷⁶⁶ normalized difference vegetation index (NDVI) in the era of popular remote sensing. J For
⁷⁶⁷ Res [Internet]. 2021 [cited 2024 Feb 14];32:1–6. Available from: <https://link.springer.com/10.1007/s11676-020-01155-1>

⁷⁶⁹ 98. Fan X, Liu Y. A global study of NDVI difference among moderate-resolution satel-
⁷⁷⁰ lite sensors. ISPRS Journal of Photogrammetry and Remote Sensing [Internet]. 2016
⁷⁷¹ [cited 2024 Feb 14];121:177–91. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S0924271616303975>

⁷⁷³ 99. Prox L, Farine D. A framework for conceptualizing dimensions of social organization
⁷⁷⁴ in mammals. Ecol Evol [Internet]. 2020 [cited 2022 Aug 23];10:791–807. Available from:
⁷⁷⁵ <https://onlinelibrary.wiley.com/doi/10.1002/ece3.5936>

- 776 100. Grant JWA. Whether or not to defend? The influence of resource distribution. *Marine
777 Behaviour and Physiology* [Internet]. 1993 [cited 2022 Feb 3];23:137–53. Available from:
778 <http://www.tandfonline.com/doi/abs/10.1080/10236249309378862>
- 779 101. Martinez-Garcia R, Fleming CH, Seppelt R, Fagan WF, Calabrese JM. How range
780 residency and long-range perception change encounter rates. *Journal of Theoretical Biology*
781 [Internet]. 2020 [cited 2022 Mar 11];498:110267. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S0022519320301223>
- 783 102. Tian F, Fensholt R, Verbesselt J, Grogan K, Horion S, Wang Y. Evaluating tem-
784 poral consistency of long-term global NDVI datasets for trend analysis. *Remote Sensing
785 of Environment* [Internet]. 2015 [cited 2024 Feb 14];163:326–40. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S0034425715001285>
- 787 103. Wood SN. Generalized additive models: An introduction with r. Second edition. Boca
788 Raton: CRC Press/Taylor & Francis Group; 2017.
- 789 104. Nathan R, Monk CT, Arlinghaus R, Adam T, Alós J, Assaf M, et al. Big-data ap-
790 proaches lead to an increased understanding of the ecology of animal movement. *Science*
791 [Internet]. 2022 [cited 2022 Mar 9];375:eabg1780. Available from: <https://www.science.org/doi/10.1126/science.abg1780>
- 793 105. Wood SN, Li Z, Shaddick G, Augustin NH. Generalized additive models for gigadata:
794 Modeling the u.k. Black smoke network daily data. *Journal of the American Statistical
795 Association* [Internet]. 2017 [cited 2022 Mar 11];112:1199–210. Available from: <https://www.tandfonline.com/doi/full/10.1080/01621459.2016.1195744>

797 106. Intergovernmental Panel On Climate Change. Climate change 2021 – the physical
798 science basis: Working group i contribution to the sixth assessment report of the intergov-
799 ernmental panel on climate change [Internet]. 1st ed. Cambridge University Press; 2023
800 [cited 2023 Jun 30]. Available from: <https://www.cambridge.org/core/product/identifier/9781009157896/type/book>

802 107. Grant PR, Grant BR, Huey RB, Johnson MTJ, Knoll AH, Schmitt J. Evolution caused
803 by extreme events. Phil Trans R Soc B [Internet]. 2017 [cited 2022 Nov 18];372:20160146.
804 Available from: <https://royalsocietypublishing.org/doi/10.1098/rstb.2016.0146>

805 108. Rypkema D, Tuljapurkar S. Modeling extreme climatic events using the generalized ex-
806 treme value (GEV) distribution. Handbook of statistics [Internet]. Elsevier; 2021 [cited
807 2023 Oct 18]. p. 39–71. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S0169716120300511>

809 109. Yao Q, Fan J, Meng J, Lucarini V, Jensen HJ, Christensen K, et al. Emergence
810 of universal scaling in weather extreme events. 2022 [cited 2022 Nov 20]; Available from:
811 <https://arxiv.org/abs/2209.02292>