

How resource abundance and stochasticity affect organisms' range sizes

Article type: Major article

Words in abstract: 199

Words in main text: 5962

Figures: 5

Tables: 0

References: 109 (updated on 2024-05-29)

Appendices: 3

Key words: energetics, environmental stochasticity, home range, range size, ctmm, simulations

1 Abstract

2 The amount of space organisms use is thought to be tightly linked to the availability of
3 resources within their habitats, such that organisms living in productive habitats generally
4 require less space than those in resource-poor habitats. This hypothesis has widespread em-
5 pirical support, but existing studies have focused primarily on responses to the mean amount
6 of resources, while responses to the variance around the mean are still largely unknown. This
7 is not a trivial oversight. Organisms adjust to variable environmental conditions, so failing
8 to consider the effects of resource (un)predictability can result in a limited understanding
9 of an organism's range size, which challenges ecological theory and applied conservation
10 alike. In this study, we leverage the available literature to provide a unifying framework and
11 hypotheses for the effect of mean and variance in resources on range sizes. Next, we use
12 simulated movement data to demonstrate how the combined effects of mean and variance
13 in resource abundance interact to shape predictable patterns in range size. Finally, we use
14 real-world tracking data on a lowland tapir (*Tapirus terrestris*) from the Brazilian Cerrado
15 to show how this framework can be applied to better understand the movement ecology of
16 free-ranging animals.

¹⁷ **Introduction**

¹⁸ The amount of resources an organism is able to access is a strong determinant of its odds
¹⁹ of survival and reproduction. Resource limitations can cause individuals to experience a
²⁰ negative energetic balance, which can then result in lower fitness (Hou et al. 2020; Le Bot
²¹ et al. 2019), altered physiology (Dai Pra et al. 2022; Rocha et al. 2021; Le Bot et al. 2019;
²² Wessling et al. 2018), lower chance of reproduction (Stefanescu, Ubach, and Wiklund 2021;
²³ Schmidt et al. 2020; Le Bot et al. 2019; Douglas and Pearce-Higgins 2014), and even death
²⁴ (Foley, Pettorelli, and Foley 2008; Berger et al. 2018). Thus, many organisms adapt their
²⁵ behaviors and/or physiology in response to changes in local resource abundance to ensure
²⁶ their needs are met.

²⁷ While there are many ways that individuals can respond to resource availability, move-
²⁸ ment represents one of the most readily available traits that species can adjust (Kacelnik,
²⁹ Krebs, and Bernstein 1992; Charnov 1976). The relationship between organisms' movement
³⁰ and resource abundance has long been of interest to biologists. In his seminal paper, Burt
³¹ (1943) considered the search for food as the primary driver for movement within an organ-
³² ism's home range. Three decades after, Southwood (1977) suggested that change in resource
³³ abundance drives how organisms decide where to live and when to reproduce. Two years
³⁴ later, Harestad and Bunnel (1979) proposed that the simplest relationship between resource
³⁵ abundance and an organism's home-range size is

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

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

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

48 Here, we refer to a location's average amount of resources as "resource abundance",
49 while we use the phrase "resource stochasticity" to indicate the variability in resources af-
50 ter accounting for changes in the mean. We argue that, on its own, a habitat's resource
51 abundance is not sufficient to assess the habitat's quality, nor make predictions about how
52 much space an organism might use. To see this, consider,, for instance, a herbivore graz-
53 ing in a grassland with relatively low but constant forage availability (i.e., low mean and
54 variance). This individual will adopt a different behavior and adaptations if it lived in a
55 desert with equally scarce forage but rare, sudden, and strong pulses of resources (i.e., low
56 mean and high stochasticity). Although these two habitats may have the same long-term
57 average resource abundance, the ephemerality of resources in the stochastic desert environ-
58 ment would promote a different selection of movement and life history strategies. In the
59 grassland, the grazer may require a large but constant home range size as it moves between
60 patches in search of food, while in the desert it may switch between dispersal in search for
61 high-resource patches and short-term range residency within patches (*sensu* Charnov 1976;
62 see Singh et al. 2012; Wheat et al. 2017; Teitelbaum and Mueller 2019). Previous studies
63 suggest that resource stochasticity may decrease organisms' fitness and landscapes' energetic
64 balances (e.g., Chevin, Lande, and Mace 2010), but there is still limited empirical evidence
65 to support this hypothesis (but see: Herfindal et al. 2005; Nilsen, Herfindal, and Linnell
66 2005; Rizzuto et al. 2021).

67 In this paper, we illustrate how an organism's range size can be expected to depend on

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

79 Resources as a random variable

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

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

⁹³ While organisms' needs vary greatly between taxonomic groups, some needs are essential
⁹⁴ for the growth, survival, and reproduction of most organisms. All heterotrophic organisms
⁹⁵ require sources of chemical energy (i.e., food), water, and various limiting nutrients (Harvey
⁹⁶ and Clutton-Brock 1981; Baldwin and Bywater 1984; Reich 2001). As the abundance of
⁹⁷ essential resources fluctuates, motile organisms can move to new locations or 'patches' to
⁹⁸ meet their requirements (Charnov 1976; J. S. Brown, Laundre, and Gurung 1999), but they
⁹⁹ must also account for costs of movement (Taylor, Heglund, and Maloij 1982).

¹⁰⁰ Fig. 1 illustrates our first of two hypotheses, which is similar to that presented by
¹⁰¹ Harestad and Bunnel (1979). When $E(R)$ is high, we expect organisms' ranges to be
¹⁰² relatively small and near the smallest amount of space required to survive (e.g., Relyea,
¹⁰³ Lawrence, and Demarais 2000; Nilsen, Herfindal, and Linnell 2005; Herfindal et al. 2005).
¹⁰⁴ Like Harestad and Bunnel (1979), we also expect organisms' range sizes to increase nonlin-
¹⁰⁵ early as $E(R)$ decreases, but we highlight that organisms may adopt different behaviors at
¹⁰⁶ low values of $E(R)$. These behaviors include maximal home range expansion (home range
¹⁰⁷ size is limited by vagility, habitat structure, competition, and predation, e.g., Rich et al.
¹⁰⁸ 2012; Dawe, Bayne, and Boutin 2014; Berger-Tal and Saltz 2019; Tórrez-Herrera, Davis,
¹⁰⁹ and Crofoot 2020), migration (Samarra et al. 2017; Middleton et al. 2018; Geremia et al.
¹¹⁰ 2019), and nomadism (Singh et al. 2012; Polansky, Kilian, and Wittemyer 2015; Teitelbaum
¹¹¹ and Mueller 2019; Nandintsetseg et al. 2019). It is unclear when organisms switch from
¹¹² range residency to migration or nomadism (or vice-versa), but understanding the gradient
¹¹³ among these types of movement is necessary for quantifying the effect of resource abundance
¹¹⁴ on organisms' range size and movement behavior (mammals: Teitelbaum et al. 2015; moose,
¹¹⁵ *Alces alces*: Singh et al. 2012; eagles, *Haliaeetus leucocephalus*: Wheat et al. 2017; Poessel
¹¹⁶ et al. 2022; lesser flamingos, *Phoeniconaias minor*: Pretorius et al. 2020). Still, species-level
¹¹⁷ changes in movement behavior are more likely to occur over evolutionary timescales than
¹¹⁸ over an organism's lifespan, since larger ranges require greater vagility, which, in turn, is

¹¹⁹ facilitated by morphological features such as hinged joints and elongated limbs (Jetz et al.
¹²⁰ 2004; Hirt et al. 2017; Andersson 2004; Samuels, Meachen, and Sakai 2013).

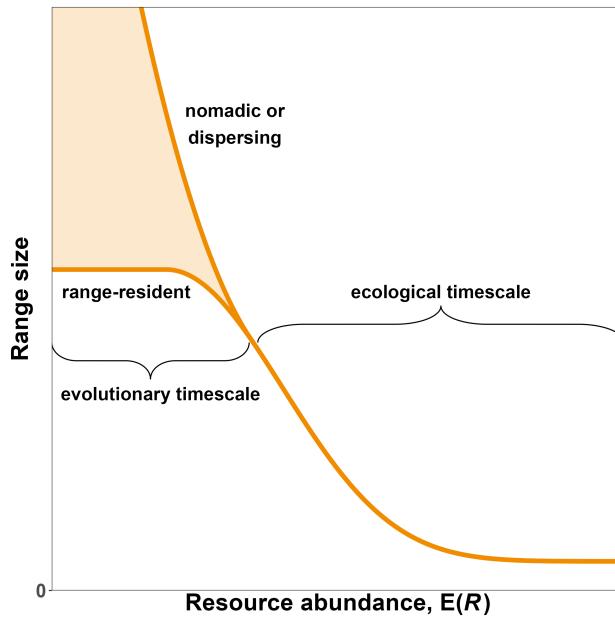


Figure 1: Hypothesized range size of an organism as a function of resource abundance, $E(R)$. We expect low values of $E(R)$ to result in a large range, since organisms are forced to explore large areas to collect the resources they require to survive, whether they be range-resident, nomadic, or migratory.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

¹²¹ Overall, the hypothesis that range size decreases with resource abundance, $E(R)$, is
¹²² commonly accepted and well supported, but many studies assume a linear relationship (e.g.,
¹²³ Relyea, Lawrence, and Demarais 2000; Rizzuto et al. 2021; Bista et al. 2022; Bradsworth et
¹²⁴ al. 2022; McClintic et al. 2014). This is problematic because, conceptually, the relationship
¹²⁵ between range size and $E(R)$ must be nonlinear, since: (1) there is an upper limit to how
¹²⁶ much space an organism is able to explore in its finite lifetime and (2) the minimum amount
¹²⁷ of space it requires to survive is necessarily greater than zero (see: Lucherini and Lovari 1996;
¹²⁸ Herfindal et al. 2005; Nilsen, Herfindal, and Linnell 2005; Simcharoen et al. 2014; Watson
¹²⁹ 2020, and contrast them to the estimates based on linear models listed above). Consequently,
¹³⁰ we suggest analysts use models that account for this nonlinearity when estimating the effects
¹³¹ of resource abundance on range size.

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

133 Assuming resource stochasticity is constant over time and space can be a useful simplification
134 of relatively stable environments or when information on how $E(R)$ changes is limited and
135 estimating changes in $\text{Var}(R)$ is unreasonable. However, such an assumption is likely not
136 realistic, since $\text{Var}(R)$ often differ across space and over time. Generally, strictly positive
137 quantities tend to have correlated mean and variances. For example, the number of berries
138 in a patch will be low during periods of scarcity (e.g., winter, droughts) due to both a low
139 mean (e.g., 15 berries) and a narrow range of values (e.g., 0 to 50 berries), which implies a
140 small variance. In contrast, periods of high productivity (e.g., spring green-up) will have a
141 higher mean (e.g., 500 berries) and wider range of R (e.g., 300 to 700 berries), which implies
142 a higher variance (e.g., due differences in phenology, environmental conditions, and patch
143 depletion). This relationship between a random variable's mean and variance is present
144 in many statistical distributions where values are strictly positive, such the Gamma and
145 Poisson distributions. See the section on probability distributions in Appendix A for more
146 information.

147 Recognizing changes in $\text{Var}(R)$ helps account for the residual, fine-scale variation in R
148 after accounting for trends in the large-scale average R (e.g., variations in plant phenology
149 between years after accounting for mean seasonal trends, see Levin 1992). However, when
150 both $E(R)$ and $\text{Var}(R)$ change over time (fig. A2), disentangling changes in $E(R)$ and $\text{Var}(R)$
151 is not simple (Steixner-Kumar and Gläscher 2020). Statistically, this is because the more
152 change one attributes to $\mu(t, u)$ (i.e., the wigglier it is), the smaller $\sigma^2(t, u)$ becomes. Con-
153 versely, the smoother $\mu(t, u)$ is, the larger $\sigma^2(t, u)$ becomes. Biologically, this is important
154 because an organism's perception scale determines whether it attributes a change in R to
155 a trend in $E(R)$ or as a stochastic event [i.e., due to $\text{Var}(R)$; see Levin (1992)]. An organ-
156 ism's perception of changes in R will also depend strongly on the its cognitive capacities
157 and memory (Mueller et al. 2013; Abrahms et al. 2019; Foley, Pettorelli, and Foley 2008;
158 Falcón-Cortés et al. 2021; Fagan et al. 2013). Whether an organism is able to predict trends

in $\sigma^2(t, u)$ or not, environmental variability is thought to reduce a landscape's energetic balance (Chevin, Lande, and Mace 2010), which, in turn, decreases organisms' fitness (e.g., Berger et al. 2018) and increases their range size. While this is true for both predictable and unpredictable stochasticity, extreme and rare events are more likely to have a stronger effect due to their unpredictability and magnitude (Logares and Nuñez 2012; Anderson et al. 2017). A few recent studies support these hypotheses (Chevin, Lande, and Mace 2010; Morellet et al. 2013; Nandintsetseg et al. 2019; Riotte-Lambert and Matthiopoulos 2020), but many of them are limited in geographic and taxonomic scales, so the extent to which these preliminary findings can be generalized is currently unknown. Thus, there remains a need for developing a more complete understanding of how organisms' range sizes changes with environmental stochasticity.

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

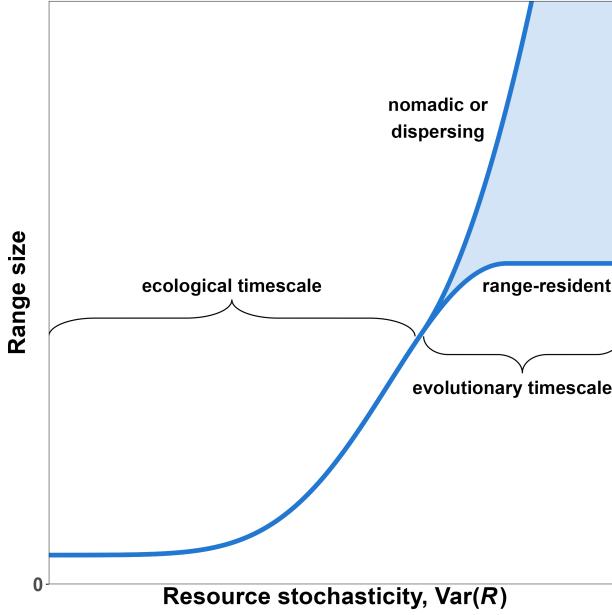


Figure 2: Hypothesized range size of an organism as a function of resource stochasticity, $\text{Var}(R)$. We expect low values of $\text{Var}(R)$ to result in small home-ranges, since organisms are able to depend on relatively predictable resources. As $\text{Var}(R)$ increases, range size should increase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

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

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

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

196 To support our hypotheses of how organisms' range sizes are affected by $E(R)$, $\text{Var}(R)$, and
197 the interaction effect of $E(R)$ and $\text{Var}(R)$, we present the results from a series of quantita-
198 tive simulations. To start, we used the `ctmm` package (Christen H. Fleming and Calabrese
199 2021) for R (R Core Team 2023) to generate 200 tracks (see Appendix B for sensitivity anal-
200 yses) from an Integrated Ornstein-Uhlenbeck movement model (IOU model, see Gurarie et
201 al. 2017). The IOU model's correlated velocity produced realistic tracks with directional
202 persistence, but, unlike Ornstein-Uhlenbeck (OU) and Ornstein-Uhlenbeck Foraging (OUF)
203 models, IOU models do not produce spatially stationary movement, so the organism is not
204 to range-resident. Consequently, each track is spatially unrestricted and can be interpreted
205 as purely exploratory or memoryless movement.

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

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

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

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

219 Consequently, we made the following assumptions:

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

238 Additional information is provided in Appendix B, including the directed acyclical graph
239 (see fig. B6 and McElreath 2016) we used to infer causal mechanisms of changes in H
240 and estimate the direct effects of $E(R)$ and $\text{Var}(R)$ on H (contrast this with fig. C5 and the
241 empirical case study below).

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

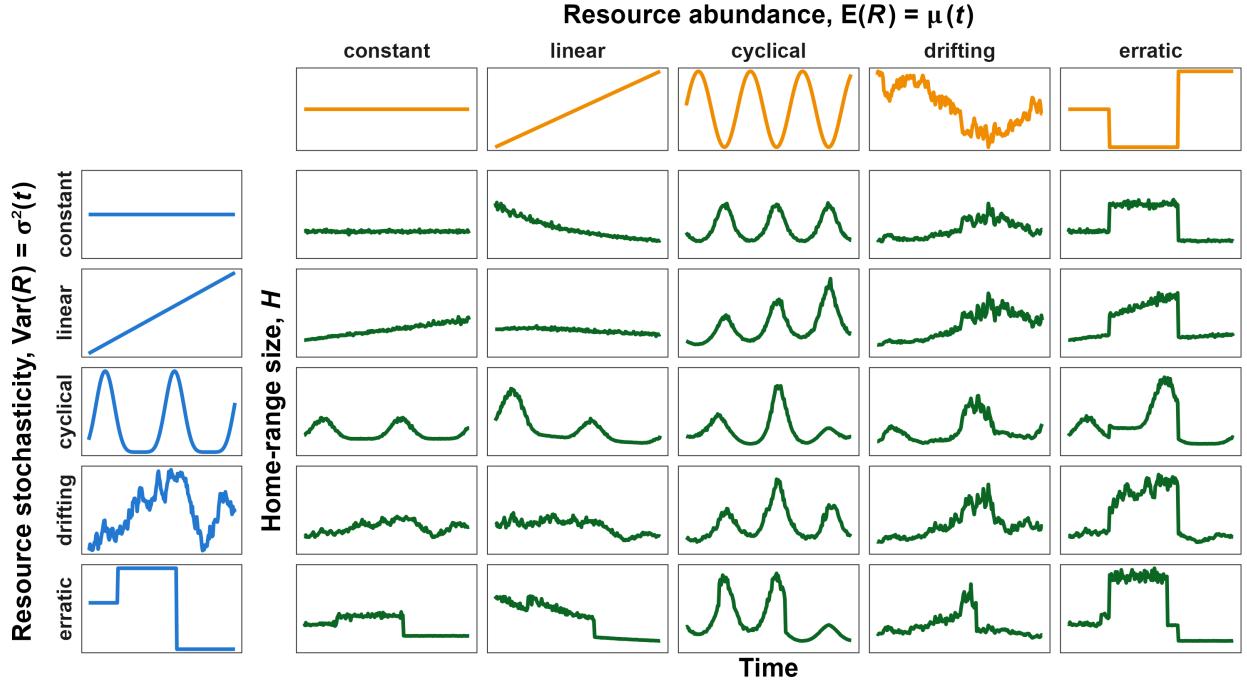


Figure 3: Simulated home-range sizes, H , of an organism living in habitats where the mean and variance in resources are constant, linearly increasing, cyclical, drifting, or erratic over time (but homogenous over space for a given t). Note how H decreases nonlinearly as $\mu(t)$ increases and increases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

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

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

The remaining panels in fig. 3 illustrate how $E(R)$ and $\text{Var}(R)$ jointly affect H and how confusing the effects can be. Since $E(R)$ and $\text{Var}(R)$ have opposite effects on H , disentangling

259 the effects can be particularly difficult when both parameters change in a correlated manner
260 (e.g., linear $E(R)$ and $\text{Var}(R)$). When both $E(R)$ and $\text{Var}(R)$ increase linearly, H initially
261 increases since the effect of $\text{Var}(R)$ is stronger, but then decreases as the effect of $E(R)$ begins
262 to dominate. Difficulties in disentangling the two effects are explored in greater depth in the
263 case study in the following section.

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

273 As expected by the changes in the spread of the points in panels A and B of fig. 4, the
274 variance in H , $\text{Var}(H)$, also depends on $E(R)$ and $\text{Var}(R)$ (fig. 4D-F). Since we modeled
275 H using a Gamma family of distributions, we expected $\text{Var}(H)$ to increase with $E(H)$, but
276 the location-scale model removes the assumption of a constant mean-variance relationship
277 (i.e., constant coefficient of variation, $\frac{\mu(t)}{\sigma^2(t)}$). This allowed us to show that the effect of R on
278 $\text{Var}(H)$ is much stronger than the effect of R on $E(H)$. Consequences of these effects are
279 explored in the discussion section.

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

281 The simulations in the section above support the hypotheses we presented in the introduction,
282 but they are based on assumptions that are often not met in real natural environments.
283 Organisms live in spatiotemporally heterogeneous and dynamic environments that promote
284 the use of perceptual ranges, navigation, and memory. Together, these abilities result in

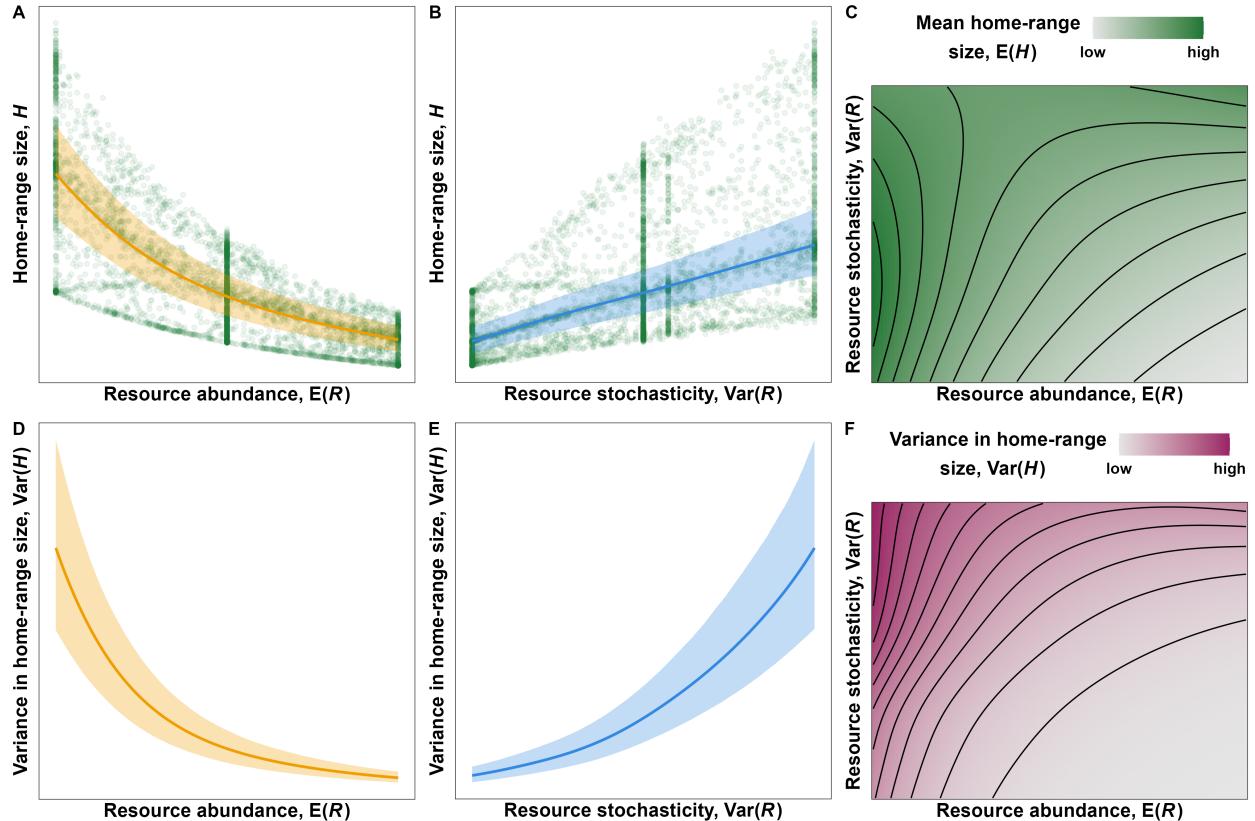


Figure 4: Effects of $E(R)$ and $\text{Var}(R)$ on the mean (A-C) and variance (D-F) in simulated home-range size with 95% Bayesian credible intervals. While the estimated marginal effect of $\text{Var}(R)$ on $E(H)$ is sublinear (panel B), the effect of $\text{Var}(R)$ is superlinear for high values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

285 selective space use that depends on resource availability (Kacelnik, Krebs, and Bernstein
286 1992) and resource depletion (Charnov 1976).

287 In this section, we test the hypotheses using empirical tracking data on a lowland tapir
288 from the Brazilian Cerrado along with empirical estimates of $E(R)$ and $\text{Var}(R)$. We mea-
289 sure R using Normalized Difference Vegetation Index (NDVI, see Pettorelli et al. 2011), a
290 remote-sensed measure of landscape greenness, as a proxy for forage abundance. Appendix
291 C contains additional information on how we modeled NDVI and the tapir’s movement us-
292 ing continuous-time movement models (Christen H. Fleming and Calabrese 2021; Noonan,
293 Fleming, et al. 2019) and autocorrelated kernel density estimation (Noonan, Tucker, et al.
294 2019; Alston et al. 2022; Silva et al. 2022).

295 Fig. 5 illustrates how a tapir in the Brazilian Cerrado adapts its 7-day home-range size to
296 spatiotemporal changes in $\mu(t, u)$ and $\sigma^2(t, u)$ (telemetry data from the individual labelled
297 as “Anna” in the dataset from Medici et al. 2022). Panels A and B show the changes in
298 seven-day average mean and variance in NDVI, respectively, experienced by the tapir during
299 the tracking period. The mean and variance in NDVI were estimated using a Generalized
300 Additive Model for Location and Scale (GAMLS, theory: Rigby and Stasinopoulos 2005;
301 Stasinopoulos and Rigby 2007; example: Gushulak et al. 2024) with a Beta family of
302 distributions (NDVI values ranged from 0.3534 to 0.9475). Panel C shows the changes in
303 the tapir’s 7-day home range over time. Note how the tapir uses more space during periods
304 of lower NDVI (e.g., August 2017) and less space during periods with high NDVI (January
305 2018). Additionally, when resources are scarce and highly unpredictable (August 2018), the
306 tapir uses up to 5 times more space than when resources are abundant and predictable (e.g.,
307 January 2018). Finally, panels D and E show the estimated (marginal) effects of $\mu(t, u)$ and
308 $\sigma^2(t, u)$ on the tapir’s 7-day home-range size. Since $\mu(t, u)$ and $\sigma^2(t, u)$ are correlated (panel
309 F) and spatiotemporally autocorrelated (panels A, B, and F), the effects of R on H should
310 be modeled carefully. To avoid over-fitting the model, we constrained the smooth effects
311 of $\mu(t, u)$ and $\sigma^2(t, u)$ and their interaction effect to a small basis size ($k = 3$). Additional

312 information is provided in appendix C. The results presented in panels D-F of fig. 5 match
313 our findings from the simulations: The tapir's 7-day home range decreases with $\mu(t, u)$ and
314 increases with $\sigma^2(t, u)$, and the effect of $\mu(t, u)$ depends on $\sigma^2(t, u)$, and vice-versa. Alone,
315 $\mu(t, u)$ and $\sigma^2(t, u)$ cause the tapir to double her home range (panels D and E), but together
316 they result in an approximate 15-fold change in home-range size (observed range: 0.8 to 12.4
317 km²; see panel F). Additionally, note how high NDVI values (> 0.8) cause $\sigma^2(t, u)$ to have
318 little to no effect on home-range size, as indicated by the vertical contour line in panel F.

319 Discussion

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

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

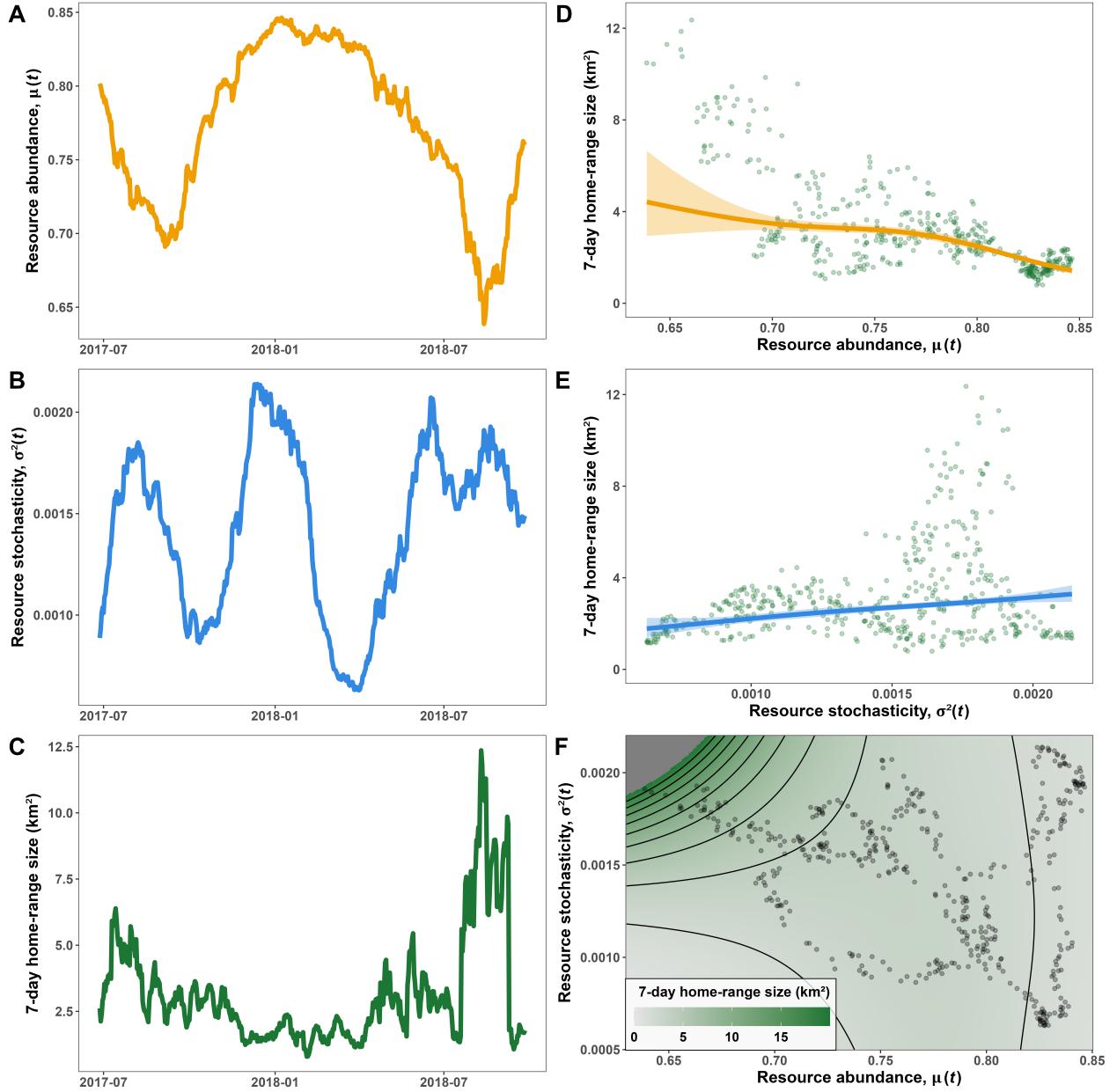


Figure 5: Effects of $\mu(t, u)$ and $\sigma^2(t, u)$ on the home-range size of a lowland tapir (*Tapirus terrestris*). (A) Trends in resource abundance over time, $\mu(t, u)$, estimated as the average mean NDVI at the locations visited by the tapir during a seven-day period. (B) Variance in resources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

338 account for real-world adaptations to $E(R)$ and $\text{Var}(R)$ such as selective space use, which
339 we account for in the empirical approach. Below we discuss the strengths and limitations of
340 each approach.

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

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

351 Deviations from the simulations offer a means of detecting when the underlying assumptions
352 are inappropriate and how additional factors may affect organisms' responses to changes
353 in $E(R)$ and $\text{Var}(R)$. For example, energetic costs of movement are often non-negligible and
354 depend on organism size (Taylor, Heglund, and Maloij 1982), movement speed (Taylor,
355 Heglund, and Maloij 1982), and ambient temperature (J. H. Brown et al. 2004; Hou et al.
356 2020). In addition, an organism may alter its movement behavior, physiology, and energetic
357 needs to buffer itself against changes in $E(R)$ and $\text{Var}(R)$ by using space selectively (Johnson
358 1980; Rickbeil et al. 2019; Riotte-Lambert and Matthiopoulos 2020; Ranc, Cagnacci, and
359 Moorcroft 2022) and adapting their behavior and physiology over time (Southwood 1977;
360 Levins 1974). Before or during periods of scarcity, organisms may cache resources (Nespolo,
361 Mejias, and Bozinovic 2022), enter states of dormancy (Goldberg and Conway 2021; Reher
362 et al. 2018), or even pause fetal growth (Schmidt et al. 2020). However, organisms may be
363 unable to respond to changes in $E(R)$ and $\text{Var}(R)$ optimally due to various reasons, includ-

ing limited perceptive range (Steixner-Kumar and Gläscher 2020), lack of experience (Foley, Pettorelli, and Foley 2008; Polansky, Kilian, and Wittemyer 2015; Falcón-Cortés et al. 2021; Merkle et al. 2019; Fagan et al. 2013; Abrahms et al. 2019), and avoidance of competitors and predators (Kacelnik, Krebs, and Bernstein 1992; Fretwell and Lucas 1969). Failure to respond optimally may thus force organisms to relocate their range to a sub-optimal location (Ciuti et al. 2012; Rich et al. 2012; Burson et al. 2018; Tórrez-Herrera, Davis, and Crofoot 2020), and may exacerbate the effects of $E(R)$ and $\text{Var}(R)$ on both mean range size and the variance around it.

Strengths and limitations of the empirical approach

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

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

390 confounding variables (S in fig. C3).

391 **HERE**

392 Examples of ecosystem-level biases are the effects of competition, predation, habitat
393 connectivity, and movement costs, all of which can depend on habitat quality, and, con-
394 sequently, be correlated nonlinearly to R and NDVI (Jetz et al. 2004; Prox and Farine
395 2020). Resource-rich patches can attract larger amounts of competitors (Kacelnik, Krebs,
396 and Bernstein 1992) and predators (Duncan et al. 2015), which may, in turn, increase pres-
397 sures from competition and predation (Charnov 1976; J. S. Brown, Laundre, and Gurung
398 1999). However, such pressures may result in both an expansion of the range (Jetz et al.
399 2004; Prox and Farine 2020) or a contraction, since larger ranges can be harder to defend
400 and result in higher movement costs (J. W. A. Grant 1993; Jetz et al. 2004) and encounter
401 rates (Martinez-Garcia et al. 2020).

402 Satellite-level confounds include information loss due to coarse spatiotemporal resolution
403 (Huang et al. 2021; Fan and Liu 2016), satellite-level error (Huang et al. 2021; Tian et al.
404 2015; Fan and Liu 2016), and other limitations of remote sensing (e.g., inability to quantify
405 specific resources or small-scale resource depletion). However, nonlinear models such as
406 Generalized Additive Models (Wood 2017) can help account for preferences for intermediate
407 values of remotely-sensed R (e.g., young grass rather than mature grasslands, see Huang et
408 al. 2021).

409 **Conclusion**

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

415 Recent advances in computational power have greatly increased analysts' ability to fit

⁴¹⁶ computationally demanding models (Nathan et al. 2022; Wood et al. 2017) that allow
⁴¹⁷ biologists to move beyond only considering changes in mean conditions. By accounting for
⁴¹⁸ changes in stochasticity, we can start developing a more comprehensive understanding of how
⁴¹⁹ organisms adapt to the dynamic environments organisms live in, including recent changes in
⁴²⁰ climate (Intergovernmental Panel On Climate Change 2023) and increases in the frequenct
⁴²¹ and intensity of extreme events (Logares and Nuñez 2012; Anderson et al. 2017; P. R. Grant
⁴²² et al. 2017; Rypkema and Tuljapurkar 2021; Yao et al. 2022).

⁴²³ **Conflict of interest**

⁴²⁴ The authors declare there are no conflicts of interest.

425 **References**

- 426 Abrahms, Briana, Elliott L. Hazen, Ellen O. Aikens, Matthew S. Savoca, Jeremy A. Gold-
427 bogen, Steven J. Bograd, Michael G. Jacox, Ladd M. Irvine, Daniel M. Palacios, and
428 Bruce R. Mate. 2019. “Memory and Resource Tracking Drive Blue Whale Migra-
429 tions.” *Proceedings of the National Academy of Sciences* 116 (12): 5582–87. <https://doi.org/10.1073/pnas.1819031116>.
- 430
- 431 Alston, Jesse M., Christen H. Fleming, Roland Kays, Jarryd P. Streicher, Colleen T.
432 Downs, Tharmalingam Ramesh, Björn Reineking, and Justin M. Calabrese. 2022.
433 “Mitigating Pseudoreplication and Bias in Resource Selection Functions with Au-
434 tocorrelation-informed Weighting.” *Methods in Ecology and Evolution*, November,
435 2041–210X.14025. <https://doi.org/10.1111/2041-210X.14025>.
- 436 Anderson, Sean C., Trevor A. Branch, Andrew B. Cooper, and Nicholas K. Dulvy. 2017.
437 “Black-Swan Events in Animal Populations.” *Proceedings of the National Academy of
438 Sciences* 114 (12): 3252–57. <https://doi.org/10.1073/pnas.1611525114>.
- 439 Andersson, Ki. 2004. “Elbow-Joint Morphology as a Guide to Forearm Function and For-
440 aging Behaviour in Mammalian Carnivores.” *Zoological Journal of the Linnean Society*
441 142 (1): 91–104. <https://doi.org/10.1111/j.1096-3642.2004.00129.x>.
- 442 Baldwin, RL, and AC Bywater. 1984. “Nutritional Energetics of Animals.” *Annual Review of
443 Nutrition* 4 (1): 101–14. <https://doi.org/https://doi.org/10.1146/annurev.nu.04.070184.000533>.
- 445 Berger, J., C. Hartway, A. Gruzdev, and M. Johnson. 2018. “Climate Degradation and
446 Extreme Icing Events Constrain Life in Cold-Adapted Mammals.” *Scientific Reports* 8
447 (1): 1156. <https://doi.org/10.1038/s41598-018-19416-9>.
- 448 Berger-Tal, Oded, and David Saltz. 2019. “Invisible Barriers: Anthropogenic Impacts on
449 Inter- and Intra-Specific Interactions as Drivers of Landscape-Independent Fragmenta-
450 tion.” *Philosophical Transactions of the Royal Society B: Biological Sciences* 374 (1781):

- 451 20180049. <https://doi.org/10.1098/rstb.2018.0049>.
- 452 Bista, Damber, Greg S. Baxter, Nicholas J. Hudson, Sonam Tashi Lama, and Peter John
453 Murray. 2022. “Effect of Disturbances and Habitat Fragmentation on an Arboreal Habi-
454 tatt Specialist Mammal Using GPS Telemetry: A Case of the Red Panda.” *Landscape*
455 *Ecology* 37 (3): 795–809. <https://doi.org/10.1007/s10980-021-01357-w>.
- 456 Bradsworth, Nick, John G. White, Anthony R. Rendall, Nicholas Carter, Desley A. Whisson,
457 and Raylene Cooke. 2022. “Using Thresholds to Determine Priorities for Apex Predator
458 Conservation in an Urban Landscape.” *Landscape and Urban Planning* 228 (December):
459 104559. <https://doi.org/10.1016/j.landurbplan.2022.104559>.
- 460 Brown, J. S., J. W. Laundre, and M. Gurung. 1999. “The Ecology of Fear: Optimal
461 Foraging, Game Theory, and Trophic Interactions.” *Journal of Mammalogy* 80 (2): 385–
462 99. <https://doi.org/10.2307/1383287>.
- 463 Brown, James H., James F. Gillooly, Andrew P. Allen, Van M. Savage, and Geoffrey B.
464 West. 2004. “Toward a Metabolic Theory of Ecology.” *Ecology* 85 (7): 1771–89. <https://doi.org/10.1890/03-9000>.
- 466 Burson, Amanda, Maayke Stomp, Emma Greenwell, Julia Grosse, and Jef Huisman. 2018.
467 “Competition for Nutrients and Light: Testing Advances in Resource Competition with a
468 Natural Phytoplankton Community.” *Ecology* 99 (5): 1108–18. <https://doi.org/10.1002/ecy.2187>.
- 470 Burt, William Henry. 1943. “Territoriality and Home Range Concepts as Applied to Mam-
471 mals.” *Journal of Mammalogy* 24 (3): 346. <https://doi.org/10.2307/1374834>.
- 472 Charnov, Eric L. 1976. “Optimal Foraging, the Marginal Value Theorem.” *Theoretical
473 Population Biology* 9 (2): 129–36. [https://doi.org/10.1016/0040-5809\(76\)90040-X](https://doi.org/10.1016/0040-5809(76)90040-X).
- 474 Chevin, Luis-Miguel, Russell Lande, and Georgina M. Mace. 2010. “Adaptation, Plasticity,
475 and Extinction in a Changing Environment: Towards a Predictive Theory.” Edited by
476 Joel G. Kingsolver. *PLoS Biology* 8 (4): e1000357. <https://doi.org/10.1371/journal.pbio.1000357>.

- 478 Ciuti, Simone, Joseph M. Northrup, Tyler B. Muhly, Silvia Simi, Marco Musiani, Justin A.
479 Pitt, and Mark S. Boyce. 2012. “Effects of Humans on Behaviour of Wildlife Exceed
480 Those of Natural Predators in a Landscape of Fear.” Edited by Nei Moreira. *PLoS ONE*
481 7 (11): e50611. <https://doi.org/10.1371/journal.pone.0050611>.
- 482 Dai Pra, Rafael, Sarah M. Mohr, Dana K. Merriman, Sviatoslav N. Bagriantsev, and Elena
483 O. Gracheva. 2022. “Ground Squirrels Initiate Sexual Maturation During Hibernation.”
484 *Current Biology* 32 (8): 1822–1828.e4. <https://doi.org/10.1016/j.cub.2022.02.032>.
- 485 Dawe, K. L., E. M. Bayne, and S. Boutin. 2014. “Influence of Climate and Human Land Use
486 on the Distribution of White-Tailed Deer (*Odocoileus Virginianus*) in the Western Boreal
487 Forest.” *Canadian Journal of Zoology* 92 (4): 353–63. <https://doi.org/10.1139/cjz-2013-0262>.
- 488 Douglas, David J. T., and James W. Pearce-Higgins. 2014. “Relative Importance of Prey
489 Abundance and Habitat Structure as Drivers of Shorebird Breeding Success and Abun-
490 dance: Drivers of Shorebird Breeding Success and Abundance.” *Animal Conservation* 17
491 (6): 535–43. <https://doi.org/10.1111/acv.12119>.
- 492 Duncan, Clare, Erlend B. Nilsen, John D. C. Linnell, and Nathalie Pettorelli. 2015.
493 “Life-history Attributes and Resource Dynamics Determine Intraspecific Home-range
494 Sizes in Carnivora.” *Remote Sensing in Ecology and Conservation* 1 (1): 39–50.
495 <https://doi.org/10.1002/rse2.6>.
- 496 Fagan, William F., Mark A. Lewis, Marie Auger-Méthé, Tal Avgar, Simon Benhamou, Greg
497 Breed, Lara LaDage, et al. 2013. “Spatial Memory and Animal Movement.” Edited by
498 Jean Clobert. *Ecology Letters* 16 (10): 1316–29. <https://doi.org/10.1111/ele.12165>.
- 499 Falcón-Cortés, Andrea, Denis Boyer, Evelyn Merrill, Jacqueline L. Frair, and Juan Manuel
500 Morales. 2021. “Hierarchical, Memory-Based Movement Models for Translocated Elk
501 (*Cervus Canadensis*).” *Frontiers in Ecology and Evolution* 9 (August): 702925. <https://doi.org/10.3389/fevo.2021.702925>.
- 502 Fan, Xingwang, and Yuanbo Liu. 2016. “A Global Study of NDVI Difference Among
503

- 505 Moderate-Resolution Satellite Sensors.” *ISPRS Journal of Photogrammetry and Remote*
506 *Sensing* 121 (November): 177–91. <https://doi.org/10.1016/j.isprsjprs.2016.09.008>.
- 507 Fjelldal, Mari Aas, Jonathan Wright, and Clare Stawski. 2021. “Nightly Torpor Use in
508 Response to Weather Conditions and Individual State in an Insectivorous Bat.” *Oecologia*
509 197 (1): 129–42. <https://doi.org/10.1007/s00442-021-05022-6>.
- 510 Fleming, Chris H., Justin M. Calabrese, Thomas Mueller, Kirk A. Olson, Peter Leimgruber,
511 and William F. Fagan. 2014. “From Fine-Scale Foraging to Home Ranges: A Semi-
512 variance Approach to Identifying Movement Modes Across Spatiotemporal Scales.” *The*
513 *American Naturalist* 183 (5): E154–67. <https://doi.org/10.1086/675504>.
- 514 Fleming, Christen H., and Justin M. Calabrese. 2021. *Ctmm: Continuous-Time Movement*
515 *Modeling*. <https://github.com/ctmm-initiative/ctmm>, <https://groups.google.com/g/ctmm-user>.
- 516
- 517 Foley, Charles, Nathalie Pettorelli, and Lara Foley. 2008. “Severe Drought and Calf Survival
518 in Elephants.” *Biology Letters* 4 (5): 541–44. <https://doi.org/10.1098/rsbl.2008.0370>.
- 519 Fretwell, Stephen Dewitt, and Henry L. Lucas. 1969. “On Territorial Behavior and Other
520 Factors Influencing Habitat Distribution in Birds: I. Theoretical Development.” *Acta*
521 *Biotheoretica* 19 (1): 16–36. <https://doi.org/10.1007/BF01601953>.
- 522 Gautam, Hansraj, Evangeline Arulmalar, Mihir R. Kulkarni, and T. N. C. Vidya. 2019.
523 “NDVI Is Not Reliable as a Surrogate of Forage Abundance for a Large Herbivore in
524 Tropical Forest Habitat.” *Biotropica* 51 (3): 443–56. <https://doi.org/10.1111/btp.12651>.
- 525 Geremia, Chris, Jerod A. Merkle, Daniel R. Eacker, Rick L. Wallen, P. J. White, Mark
526 Hebblewhite, and Matthew J. Kauffman. 2019. “Migrating Bison Engineer the Green
527 Wave.” *Proceedings of the National Academy of Sciences* 116 (51): 25707–13. <https://doi.org/10.1073/pnas.1913783116>.
- 528
- 529 Goldberg, Amanda R., and Courtney J Conway. 2021. “Hibernation Behavior of a Feder-
530 ally Threatened Ground Squirrel: Climate Change and Habitat Selection Implications.”
531 Edited by Loren Hayes. *Journal of Mammalogy* 102 (2): 574–87. <https://doi.org/10>.

- 532 1093/jmammal/gyab021.
- 533 Grant, James W. A. 1993. "Whether or Not to Defend? The Influence of Resource Dis-
534 tribution." *Marine Behaviour and Physiology* 23 (1): 137–53. <https://doi.org/10.1080/10236249309378862>.
- 535
- 536 Grant, Peter R., B. Rosemary Grant, Raymond B. Huey, Marc T. J. Johnson, Andrew H.
537 Knoll, and Johanna Schmitt. 2017. "Evolution Caused by Extreme Events." *Philoso-
538 sophical Transactions of the Royal Society B: Biological Sciences* 372 (1723): 20160146.
539 <https://doi.org/10.1098/rstb.2016.0146>.
- 540 Gurarie, Eliezer, Christen H. Fleming, William F. Fagan, Kristin L. Laidre, Jesús Hernández-
541 Pliego, and Otso Ovaskainen. 2017. "Correlated Velocity Models as a Fundamental
542 Unit of Animal Movement: Synthesis and Applications." *Movement Ecology* 5 (1): 13.
543 <https://doi.org/10.1186/s40462-017-0103-3>.
- 544 Gushulak, Cale A. C., Stefano Mezzini, Katherine E. Moir, Gavin L. Simpson, Lynda
545 Bunting, Björn Wissel, Daniel R. Engstrom, et al. 2024. "Impacts of a Century of
546 Land-use Change on the Eutrophication of Large, Shallow, Prairie Lake Manitoba in
547 Relation to Adjacent Lake Winnipeg (Manitoba, Canada)." *Freshwater Biology* 69 (1):
548 47–63. <https://doi.org/10.1111/fwb.14192>.
- 549 Harestad, A. S., and F. L. Bunnel. 1979. "Home Range and Body Weight—a Reevaluation."
550 *Ecology* 60 (2): 389–402. <https://doi.org/10.2307/1937667>.
- 551 Harvey, Paul H., and T. H. Clutton-Brock. 1981. "Primate Home-Range Size and Metabolic
552 Needs." *Behavioral Ecology and Sociobiology* 8 (2): 151–55. <https://doi.org/10.1007/BF00300828>.
- 553
- 554 Herfindal, Ivar, John D. C. Linnell, John Odden, Erlend Birkeland Nilsen, and Reidar
555 Andersen. 2005. "Prey Density, Environmental Productivity and Home-range Size
556 in the Eurasian Lynx (*Lynx Lynx*)." *Journal of Zoology* 265 (1): 63–71. <https://doi.org/10.1017/S0952836904006053>.
- 557
- 558 Hirt, Myriam R., Walter Jetz, Björn C. Rall, and Ulrich Brose. 2017. "A General Scaling

- 559 Law Reveals Why the Largest Animals Are Not the Fastest.” *Nature Ecology & Evolution*
560 1 (8): 1116–22. <https://doi.org/10.1038/s41559-017-0241-4>.
- 561 Hou, Rong, Colin A. Chapman, Ollie Jay, Songtao Guo, Baoguo Li, and David Rauben-
562 heimer. 2020. “Cold and Hungry: Combined Effects of Low Temperature and Resource
563 Scarcity on an Edge-of-range Temperate Primate, the Golden Snub-nose Monkey.” *Eco-
564 graphy* 43 (11): 1672–82. <https://doi.org/10.1111/ecog.05295>.
- 565 Huang, Sha, Lina Tang, Joseph P. Hupy, Yang Wang, and Guofan Shao. 2021. “A
566 Commentary Review on the Use of Normalized Difference Vegetation Index (NDVI)
567 in the Era of Popular Remote Sensing.” *Journal of Forestry Research* 32 (1): 1–6.
568 <https://doi.org/10.1007/s11676-020-01155-1>.
- 569 Intergovernmental Panel On Climate Change. 2023. *Climate Change 2021 – the Physical
570 Science Basis: Working Group i Contribution to the Sixth Assessment Report of the
571 Intergovernmental Panel on Climate Change*. 1st ed. Cambridge University Press. <https://doi.org/10.1017/9781009157896>.
- 572 Jetz, Walter, Chris Carbone, Jenny Fulford, and James H. Brown. 2004. “The Scaling
573 of Animal Space Use.” *Science* 306 (5694): 266–68. <https://doi.org/10.1126/science.1102138>.
- 574 Johnson, Douglas H. 1980. “The Comparison of Usage and Availability Measurements
575 for Evaluating Resource Preference.” *Ecology* 61 (1): 65–71. <https://doi.org/10.2307/1937156>.
- 576 Kacelnik, Alejandro, John R. Krebs, and Carlos Bernstein. 1992. “The Ideal Free Distri-
577 bution and Predator-Prey Populations.” *Trends in Ecology & Evolution* 7 (2): 50–55.
578 [https://doi.org/10.1016/0169-5347\(92\)90106-L](https://doi.org/10.1016/0169-5347(92)90106-L).
- 579 Le Bot, Tangi, Amélie Lescroël, Jérôme Fort, Clara Péron, Olivier Gimenez, Pascal Provost,
580 and David Grémillet. 2019. “Fishery Discards Do Not Compensate Natural Prey Short-
581 age in Northern Gannets from the English Channel.” *Biological Conservation* 236 (Au-
582 gust): 375–84. <https://doi.org/10.1016/j.biocon.2019.05.040>.

- 586 Levin, Simon A. 1992. "The Problem of Pattern and Scale in Ecology: The Robert h.
587 MacArthur Award Lecture." *Ecology* 73 (6): 1943–67. <https://doi.org/10.2307/1941447>.
- 588 Levins, Richard A. 1974. *Evolution in Changing Environments: Some Theoretical Explorations*. 3. printing. Monographs in Population Biology 2. Princeton, NJ: Princeton
589 Univ. Press.
- 590
- 591 Lindstedt, Stan L., and Mark S. Boyce. 1985. "Seasonality, Fasting Endurance, and Body
592 Size in Mammals." *The American Naturalist* 125 (6): 873–78. <https://doi.org/10.1086/284385>.
- 593
- 594 Logares, Ramiro, and Martin Nuñez. 2012. "Black Swans in Ecology and Evolution: The
595 Importance of Improbable but Highly Influential Events." *Ideas in Ecology and Evolution*.
596 <https://doi.org/10.4033/iee.2012.5.5.n>.
- 597 Lucherini, M., and S. Lovari. 1996. "Habitat Richness Affects Home Range Size in the Red
598 Fox *Vulpes Vulpes*." *Behavioural Processes* 36 (1): 103–5. [https://doi.org/10.1016/0376-6357\(95\)00018-6](https://doi.org/10.1016/0376-6357(95)00018-6).
- 599
- 600 Martinez-Garcia, Ricardo, Christen H. Fleming, Ralf Seppelt, William F. Fagan, and Justin
601 M. Calabrese. 2020. "How Range Residency and Long-Range Perception Change Enc-
602 counter Rates." *Journal of Theoretical Biology* 498 (August): 110267. <https://doi.org/10.1016/j.jtbi.2020.110267>.
- 603
- 604 McClintic, L. F., J. D. Taylor, J. C. Jones, R. D. Singleton, and G. Wang. 2014. "Effects
605 of Spatiotemporal Resource Heterogeneity on Home Range Size of American Beaver."
606 *Journal of Zoology* 293 (2): 134–41. <https://doi.org/10.1111/jzo.12128>.
- 607 McElreath, Richard. 2016. *Statistical Rethinking: A Bayesian Course with Examples in r
and Stan*. Chapman & Hall/CRC Texts in Statistical Science Series 122. Boca Raton:
608 CRC Press/Taylor & Francis Group.
- 609
- 610 Medici, E. P., S. Mezzini, C. H. Fleming, J. M. Calabrese, and M. J. Noonan. 2022. "Move-
611 ment Ecology of Vulnerable Lowland Tapirs Between Areas of Varying Human Distur-
612 bance." *Movement Ecology* 10 (1): 14. <https://doi.org/10.1186/s40462-022-00313-w>.

- 613 Merkle, Jerod A., Kevin L. Monteith, Ellen O. Aikens, Matthew M. Hayes, Kent R.
614 Hersey, Arthur D. Middleton, Brendan A. Oates, Hall Sawyer, Brandon M. Scurlock,
615 and Matthew J. Kauffman. 2016. "Large Herbivores Surf Waves of Green-up During
616 Spring." *Proceedings of the Royal Society B: Biological Sciences* 283 (1833): 20160456.
617 <https://doi.org/10.1098/rspb.2016.0456>.
- 618 Merkle, Jerod A., Hall Sawyer, Kevin L. Monteith, Samantha P. H. Dwinnell, Gary L.
619 Fralick, and Matthew J. Kauffman. 2019. "Spatial Memory Shapes Migration and Its
620 Benefits: Evidence from a Large Herbivore." Edited by Jean-Michel Gaillard. *Ecology*
621 *Letters* 22 (11): 1797–1805. <https://doi.org/10.1111/ele.13362>.
- 622 Middleton, Arthur D., Jerod A. Merkle, Douglas E. McWhirter, John G. Cook, Rachel C.
623 Cook, P. J. White, and Matthew J. Kauffman. 2018. "Green-Wave Surfing Increases Fat
624 Gain in a Migratory Ungulate." *Oikos* 127 (7): 1060–68. <https://doi.org/10.1111/oik.05227>.
- 626 Morellet, Nicolas, Christophe Bonenfant, Luca Börger, Federico Ossi, Francesca Cagnacci,
627 Marco Heurich, Petter Kjellander, et al. 2013. "Seasonality, Weather and Climate Affect
628 Home Range Size in Roe Deer Across a Wide Latitudinal Gradient Within Europe."
629 Edited by Tim Coulson. *Journal of Animal Ecology* 82 (6): 1326–39. <https://doi.org/10.1111/1365-2656.12105>.
- 631 Mueller, Thomas, Robert B. O'Hara, Sarah J. Converse, Richard P. Urbanek, and William
632 F. Fagan. 2013. "Social Learning of Migratory Performance." *Science* 341 (6149): 999–
633 1002. <https://doi.org/10.1126/science.1237139>.
- 634 Nandintsetseg, Dejid, Chloe Bracis, Peter Leimgruber, Petra Kaczensky, Bayarbaatar Bu-
635 uveibaatar, Badamjav Lkhagvasuren, Buyanaa Chimeddorj, et al. 2019. "Variability
636 in Nomadism: Environmental Gradients Modulate the Movement Behaviors of Dryland
637 Ungulates." *Ecosphere* 10 (11). <https://doi.org/10.1002/ecs2.2924>.
- 638 Nathan, Ran, Wayne M. Getz, Eloy Revilla, Marcel Holyoak, Ronen Kadmon, David Saltz,
639 and Peter E. Smouse. 2008. "A Movement Ecology Paradigm for Unifying Organismal

- 640 Movement Research.” *Proceedings of the National Academy of Sciences* 105 (49): 19052–
641 59. <https://doi.org/10.1073/pnas.0800375105>.
- 642 Nathan, Ran, Christopher T. Monk, Robert Arlinghaus, Timo Adam, Josep Alós, Michael
643 Assaf, Henrik Baktoft, et al. 2022. “Big-Data Approaches Lead to an Increased Under-
644 standing of the Ecology of Animal Movement.” *Science* 375 (6582): eabg1780. <https://doi.org/10.1126/science.abg1780>.
- 645
- 646 Nespolo, Roberto F., Carlos Mejias, and Francisco Bozinovic. 2022. “Why Bears Hibernate?
647 Redefining the Scaling Energetics of Hibernation.” *Proceedings of the Royal Society B:
648 Biological Sciences* 289 (1973): 20220456. <https://doi.org/10.1098/rspb.2022.0456>.
- 649 Nilsen, Erlend B., Ivar Herfindal, and John D. C. Linnell. 2005. “Can Intra-Specific Vari-
650 ation in Carnivore Home-Range Size Be Explained Using Remote-Sensing Estimates of
651 Environmental Productivity?” *Écoscience* 12 (1): 68–75. [https://doi.org/10.2980/i1195-6860-12-1-68.1](https://doi.org/10.2980/i1195-
652 6860-12-1-68.1).
- 653 Noonan, Michael J., Christen H. Fleming, Thomas S. Akre, Jonathan Drescher-Lehman,
654 Eliezer Gurarie, Autumn-Lynn Harrison, Roland Kays, and Justin M. Calabrese. 2019.
655 “Scale-Insensitive Estimation of Speed and Distance Traveled from Animal Tracking
656 Data.” *Movement Ecology* 7 (1): 35. <https://doi.org/10.1186/s40462-019-0177-1>.
- 657 Noonan, Michael J., Marlee A. Tucker, Christen H. Fleming, Thomas S. Akre, Susan C.
658 Alberts, Abdullahi H. Ali, Jeanne Altmann, et al. 2019. “A Comprehensive Analysis
659 of Autocorrelation and Bias in Home Range Estimation.” *Ecological Monographs* 89 (2):
660 e01344. <https://doi.org/10.1002/ecm.1344>.
- 661 Pettorelli, N, S Ryan, T Mueller, N Bunnefeld, B Jedrzejewska, M Lima, and K Kausrud.
662 2011. “The Normalized Difference Vegetation Index (NDVI): Unforeseen Successes in
663 Animal Ecology.” *Climate Research* 46 (1): 15–27. <https://doi.org/10.3354/cr00936>.
- 664 Phillips, Linda B., Andrew J. Hansen, and Curtis H. Flather. 2008. “Evaluating the Species
665 Energy Relationship with the Newest Measures of Ecosystem Energy: NDVI Versus
666 MODIS Primary Production.” *Remote Sensing of Environment* 112 (12): 4381–92. <https://doi.org/10.1016/j.rse.2008.07.011>.

- 667 //doi.org/10.1016/j.rse.2008.08.002.
- 668 Poessel, Sharon A., Brian Woodbridge, Brian W. Smith, Robert K. Murphy, Bryan E.
669 Bedrosian, Douglas A. Bell, David Bittner, et al. 2022. "Interpreting Long-distance
670 Movements of Non-migratory Golden Eagles: Prospecting and Nomadism?" *Ecosphere*
671 13 (6). <https://doi.org/10.1002/ecs2.4072>.
- 672 Polansky, Leo, Werner Kilian, and George Wittemyer. 2015. "Elucidating the Significance
673 of Spatial Memory on Movement Decisions by African Savannah Elephants Using State–
674 Space Models." *Proceedings of the Royal Society B: Biological Sciences* 282 (1805):
675 20143042. <https://doi.org/10.1098/rspb.2014.3042>.
- 676 Pretorius, Mattheuns D., Lourens Leeuwner, Gareth J. Tate, André Botha, Michael D.
677 Michael, Kaajial Durgaparsad, and Kishaylin Chetty. 2020. "Movement Patterns of
678 Lesser Flamingos *Phoeniconaias Minor* : Nomadism or Partial Migration?" *Wildlife
679 Biology* 2020 (3): 1–11. <https://doi.org/10.2981/wlb.00728>.
- 680 Prox, Lea, and Damien Farine. 2020. "A Framework for Conceptualizing Dimensions of
681 Social Organization in Mammals." *Ecology and Evolution* 10 (2): 791–807. <https://doi.org/10.1002/ece3.5936>.
- 683 R Core Team. 2023. *R: A Language and Environment for Statistical Computing*. Vienna,
684 Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>.
- 685 Ranc, Nathan, Francesca Cagnacci, and Paul R. Moorcroft. 2022. "Memory Drives the
686 Formation of Animal Home Ranges: Evidence from a Reintroduction." Edited by Tim
687 Coulson. *Ecology Letters* 25 (4): 716–28. <https://doi.org/10.1111/ele.13869>.
- 688 Reher, Stephanie, Julian Ehlers, Hajatiana Rabarison, and Kathrin H. Dausmann. 2018.
689 "Short and Hyperthermic Torpor Responses in the Malagasy Bat *Macronycteris Commer-*
690 *soni* Reveal a Broader Hypometabolic Scope in Heterotherms." *Journal of Comparative
691 Physiology B* 188 (6): 1015–27. <https://doi.org/10.1007/s00360-018-1171-4>.
- 692 Reich, Peter B. 2001. "Body Size, Geometry, Longevity and Metabolism: Do Plant Leaves
693 Behave Like Animal Bodies?" *Trends in Ecology & Evolution* 16 (12): 674–80. <https://doi.org/10.1006/tree.2001.1006>.

- 694 //doi.org/10.1016/S0169-5347(01)02306-0.
- 695 Relyea, Rick A., Richard K. Lawrence, and Stephen Demarais. 2000. "Home Range of
696 Desert Mule Deer: Testing the Body-Size and Habitat-Productivity Hypotheses." *The*
697 *Journal of Wildlife Management* 64 (1): 146. <https://doi.org/10.2307/3802984>.
- 698 Rich, Lindsey N., Michael S. Mitchell, Justin A. Gude, and Carolyn A. Sime. 2012. "An-
699 thropogenic Mortality, Intraspecific Competition, and Prey Availability Influence Ter-
700 ritory Sizes of Wolves in Montana." *Journal of Mammalogy* 93 (3): 722–31. <https://doi.org/10.1644/11-MAMM-A-079.2>.
- 701 Rickbeil, Gregory J. M., Jerod A. Merkle, Greg Anderson, M. Paul Atwood, Jon P. Beck-
702 mann, Eric K. Cole, Alyson B. Courtemanch, et al. 2019. "Plasticity in Elk Migration
703 Timing Is a Response to Changing Environmental Conditions." *Global Change Biology*
704 25 (7): 2368–81. <https://doi.org/10.1111/gcb.14629>.
- 705 Rigby, R. A., and D. M. Stasinopoulos. 2005. "Generalized Additive Models for Location,
706 Scale and Shape (with Discussion)." *Journal of the Royal Statistical Society: Series C*
707 (*Applied Statistics*) 54 (3): 507–54. <https://doi.org/10.1111/j.1467-9876.2005.00510.x>.
- 708 Riotte-Lambert, Louise, and Jason Matthiopoulos. 2020. "Environmental Predictability as
709 a Cause and Consequence of Animal Movement." *Trends in Ecology & Evolution* 35 (2):
710 163–74. <https://doi.org/10.1016/j.tree.2019.09.009>.
- 711 Rizzuto, Matteo, Shawn J. Leroux, Eric Vander Wal, Isabella C. Richmond, Travis R. Heck-
712 ford, Juliana Balluffi-Fry, and Yolanda F. Wiersma. 2021. "Forage Stoichiometry Pre-
713 dicts the Home Range Size of a Small Terrestrial Herbivore." *Oecologia* 197 (2): 327–38.
714 <https://doi.org/10.1007/s00442-021-04965-0>.
- 715 Rocha, Joana L., Raquel Godinho, José C. Brito, and Rasmus Nielsen. 2021. "Life in
716 Deserts: The Genetic Basis of Mammalian Desert Adaptation." *Trends in Ecology &*
717 *Evolution* 36 (7): 637–50. <https://doi.org/10.1016/j.tree.2021.03.007>.
- 718 Rypkema, Diana, and Shripad Tuljapurkar. 2021. "Modeling Extreme Climatic Events
719 Using the Generalized Extreme Value (GEV) Distribution." In *Handbook of Statistics*,

- 721 44:39–71. Elsevier. <https://doi.org/10.1016/bs.host.2020.12.002>.
- 722 Samarra, Filipa I. P., S. B. Tavares, J. Béesau, V. B. Deecke, A. Fennell, P. J. O. Miller, H.
723 Pétursson, J. Sigurjónsson, and G. A. Víkingsson. 2017. “Movements and Site Fidelity
724 of Killer Whales (*Orcinus Orca*) Relative to Seasonal and Long-Term Shifts in Herring
725 (*Clupea Harengus*) Distribution.” *Marine Biology* 164 (8): 159. <https://doi.org/10.1007/s00227-017-3187-9>.
- 726
- 727 Samuels, Joshua X., Julie A. Meachen, and Stacey A. Sakai. 2013. “Postcranial Morphology
728 and the Locomotor Habits of Living and Extinct Carnivorans.” *Journal of Morphology*
729 274 (2): 121–46. <https://doi.org/10.1002/jmor.20077>.
- 730 Schmidt, Niels M., Carsten Grøndahl, Alina L. Evans, Jean-Pierre Desforges, John Blake,
731 Lars H. Hansen, Larissa T. Beumer, et al. 2020. “On the Interplay Between Hypothermia
732 and Reproduction in a High Arctic Ungulate.” *Scientific Reports* 10 (1): 1514. <https://doi.org/10.1038/s41598-020-58298-8>.
- 733
- 734 Seigle-Ferrand, Juliette, Kamal Atmeh, Jean-Michel Gaillard, Victor Ronget, Nicolas Morel-
735 let, Mathieu Garel, Anne Loison, and Glenn Yannic. 2021. “A Systematic Review of
736 Within-Population Variation in the Size of Home Range Across Ungulates: What Do
737 We Know After 50 Years of Telemetry Studies?” *Frontiers in Ecology and Evolution* 8
738 (January): 555429. <https://doi.org/10.3389/fevo.2020.555429>.
- 739
- 740 Silva, Inês, Christen H. Fleming, Michael J. Noonan, Jesse Alston, Cody Folta, William F.
741 Fagan, and Justin M. Calabrese. 2022. “Autocorrelation-informed Home Range Estima-
742 tion: A Review and Practical Guide.” *Methods in Ecology and Evolution* 13 (3): 534–44.
<https://doi.org/10.1111/2041-210X.13786>.
- 743
- 744 Simcharoen, Achara, Tommaso Savini, George A. Gale, Saksit Simcharoen, Somphot
745 Duangchantrasiri, Somporn Pakpien, and James L. D. Smith. 2014. “Female Tiger
746 *Panthera Tigris* Home Range Size and Prey Abundance: Important Metrics for
Management.” *Oryx* 48 (3): 370–77. <https://doi.org/10.1017/S0030605312001408>.
- 747 Singh, Navinder J., Luca Börger, Holger Dettki, Nils Bunnefeld, and Göran Ericsson. 2012.

- 748 "From Migration to Nomadism: Movement Variability in a Northern Ungulate Across Its
749 Latitudinal Range." *Ecological Applications* 22 (7): 2007–20. <https://doi.org/10.1890/12-0245.1>.
- 750
- 751 Southwood, T. R. E. 1977. "Habitat, the Templet for Ecological Strategies?" *The Journal*
752 *of Animal Ecology* 46 (2): 336. <https://doi.org/10.2307/3817>.
- 753 Stasinopoulos, Mikis D., and Robert A. Rigby. 2007. "Generalized Additive Models for
754 Location Scale and Shape (GAMLSS) in r." *Journal of Statistical Software* 23 (7).
- 755 Stefanescu, Constantí, Andreu Ubach, and Christer Wiklund. 2021. "Timing of Mating,
756 Reproductive Status and Resource Availability in Relation to Migration in the Painted
757 Lady Butterfly." *Animal Behaviour* 172 (February): 145–53. <https://doi.org/10.1016/j.anbehav.2020.12.013>.
- 758
- 759 Steixner-Kumar, Saurabh, and Jan Gläscher. 2020. "Strategies for Navigating a Dynamic
760 World." *Science* 369 (6507): 1056–57. <https://doi.org/10.1126/science.abd7258>.
- 761 Stephens, D. W., and Eric L. Charnov. 1982. "Optimal Foraging: Some Simple Stochastic
762 Models." *Behavioral Ecology and Sociobiology* 10 (4): 251–63. <https://doi.org/10.1007/BF00302814>.
- 763
- 764 Taylor, C. R., N. C. Heglund, and G. M. Maloiy. 1982. "Energetics and Mechanics of
765 Terrestrial Locomotion. I. Metabolic Energy Consumption as a Function of Speed and
766 Body Size in Birds and Mammals." *Journal of Experimental Biology* 97 (1): 1–21. <https://doi.org/10.1242/jeb.97.1.1>.
- 767
- 768 Teitelbaum, Claire S., William F. Fagan, Chris H. Fleming, Gunnar Dressler, Justin M. Cal-
769 abrese, Peter Leimgruber, and Thomas Mueller. 2015. "How Far to Go? Determinants
770 of Migration Distance in Land Mammals." Edited by Marco Festa-Bianchet. *Ecology*
771 *Letters* 18 (6): 545–52. <https://doi.org/10.1111/ele.12435>.
- 772
- 773 Teitelbaum, Claire S., and Thomas Mueller. 2019. "Beyond Migration: Causes and Conse-
774 quences of Nomadic Animal Movements." *Trends in Ecology & Evolution* 34 (6): 569–81.
<https://doi.org/10.1016/j.tree.2019.02.005>.

- 775 Tian, Feng, Rasmus Fensholt, Jan Verbesselt, Kenneth Grogan, Stephanie Horion, and
776 Yunjia Wang. 2015. “Evaluating Temporal Consistency of Long-Term Global NDVI
777 Datasets for Trend Analysis.” *Remote Sensing of Environment* 163 (June): 326–40.
778 <https://doi.org/10.1016/j.rse.2015.03.031>.
- 779 Tórrez-Herrera, Lucía L., Grace H. Davis, and Margaret C. Crofoot. 2020. “Do Monkeys
780 Avoid Areas of Home Range Overlap Because They Are Dangerous? A Test of the
781 Risk Hypothesis in White-Faced Capuchin Monkeys (*Cebus Capucinus*).” *International
782 Journal of Primatology* 41 (2): 246–64. <https://doi.org/10.1007/s10764-019-00110-0>.
- 783 Van Baalen, Minus, Vlastimil Křivan, Paul C. J. Van Rijn, and Maurice W. Sabelis. 2001.
784 “Alternative Food, Switching Predators, and the Persistence of Predator-prey Systems.”
785 *The American Naturalist* 157 (5): 512–24. <https://doi.org/10.1086/319933>.
- 786 Watson, Jesse. 2020. “Ferruginous Hawk (*Buteo Regalis*) Home Range and Resource Use
787 on Northern Grasslands in Canada.” <https://doi.org/10.13140/RG.2.2.32404.32648>.
- 788 Wessling, Erin G., Tobias Deschner, Roger Mundry, Jill D. Pruetz, Roman M. Wittig, and
789 Hjalmar S. Kühl. 2018. “Seasonal Variation in Physiology Challenges the Notion of
790 Chimpanzees (*Pan Troglodytes Verus*) as a Forest-Adapted Species.” *Frontiers in Ecology
791 and Evolution* 6 (May): 60. <https://doi.org/10.3389/fevo.2018.00060>.
- 792 Wheat, Rachel E., Stephen B. Lewis, Yiwei Wang, Taal Levi, and Christopher C. Wilmers.
793 2017. “To Migrate, Stay Put, or Wander? Varied Movement Strategies in Bald Ea-
794 gles (*Haliaeetus Leucocephalus*).” *Movement Ecology* 5 (1): 9. <https://doi.org/10.1186/s40462-017-0102-4>.
- 795 Wood, Simon N. 2017. *Generalized Additive Models: An Introduction with r*. Second edition.
796 Chapman & Hall/CRC Texts in Statistical Science. Boca Raton: CRC Press/Taylor &
797 Francis Group.
- 798 Wood, Simon N., Zheyuan Li, Gavin Shaddick, and Nicole H. Augustin. 2017. “Generalized
799 Additive Models for Gigadata: Modeling the u.k. Black Smoke Network Daily Data.”
800 *Journal of the American Statistical Association* 112 (519): 1199–1210. <https://doi.org/>

802 10.1080/01621459.2016.1195744.

803 Yao, Qing, Jingfang Fan, Jun Meng, Valerio Lucarini, Henrik Jeldtoft Jensen, Kim Chris-
804 tensen, and Xiaosong Chen. 2022. “Emergence of Universal Scaling in Weather Extreme
805 Events.” <https://doi.org/10.48550/ARXIV.2209.02292>.