

# How resource abundance and stochasticity affect organisms' range sizes

Stefano Mezzini<sup>1,2</sup>

Chris H. Fleming<sup>3,4</sup>

E. Patrícia Medici<sup>5,6,7</sup>

Michael J. Noonan<sup>1,2,8,\*</sup>

<sup>1</sup> Okanagan Institute for Biodiversity, Resilience, and Ecosystem Services, The University of British Columbia Okanagan, Kelowna, British Columbia, Canada.

<sup>2</sup> Department of Biology, The University of British Columbia Okanagan, Kelowna, British Columbia, Canada.

<sup>3</sup> Department of Biology, University of Central Florida, Orlando, Florida 32816, United States.

<sup>4</sup> Smithsonian Conservation Biology Institute, National Zoological Park, 1500 Remount Rd., Front Royal, VA 22630, United States.

<sup>5</sup> Lowland Tapir Conservation Initiative (LTCI), Instituto de Pesquisas Ecológicas (IPÊ), Rodovia Dom Pedro I, km 47, Nazaré Paulista, São Paulo 12960-000, Brazil.

<sup>6</sup> IUCN SSC Tapir Specialist Group (TSG), Campo Grande, Brazil.

<sup>7</sup> Escola Superior de Conservação Ambiental E Sustentabilidade (ESCAS/IPÊ), Rodovia Dom Pedro I, km 47, Nazaré Paulista, São Paulo 12960-000, Brazil.

<sup>8</sup> Department of Computer Science, Math, Physics, and Statistics, The University of British Columbia Okanagan, Kelowna, British Columbia, Canada.

\* Correspondence: Michael J. Noonan <michael.noonan@ubc.ca>

**Article type:** Major article

**Words in abstract:** 199

**Words in main text:** 6028

**Figures:** 5

**Tables:** 0

**References:** 107 (updated on 2024-07-22)

**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.

<sub>17</sub> **Introduction**

<sub>18</sub> The amount of resources an organism is able to access is a strong determinant of its odds  
<sub>19</sub> of survival and reproduction. Resource limitations can cause individuals to experience a  
<sub>20</sub> negative energetic balance, which can then result in lower fitness [1,2], altered physiology  
<sub>21</sub> [2–5], lower chance of reproduction [2,6–8], and even death [9,10]. Thus, many organisms  
<sub>22</sub> adapt their behaviors and/or physiology in response to changes in local resource abundance  
<sub>23</sub> to ensure their needs are met.

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

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

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

41 17,18,19]. Thus, there remains a need for clear hypotheses of the effects of both resource  
42 abundance and stochasticity on organisms' range sizes.

43 Here, we refer to a location's average amount of resources as "resource abundance",  
44 while we use the phrase "resource stochasticity" to indicate the variability in resources after  
45 accounting for changes in the mean. We argue that, on its own, a habitat's resource abun-  
46 dance is not sufficient to assess the habitat's quality, nor make predictions about how much  
47 space an organism might use. To see this, consider, for instance, a herbivore grazing in a  
48 grassland with relatively low but constant forage availability (i.e., low mean and variance).  
49 This individual will adopt different behaviors and adaptations if it lived in a desert with  
50 equally scarce forage but rare, sudden, and strong pulses of resources (i.e., low mean and  
51 high stochasticity). In the grassland, the grazer may require a large but constant home  
52 range size as it moves between patches in search of food, while in the desert it may switch  
53 between dispersal in search for high-resource patches and short-term range residency within  
54 patches [*sensu* 12,see 20,21,22]. Previous studies suggest that resource stochasticity may  
55 decrease organisms' fitness and landscapes' energetic balances [e.g., 23], but there is still  
56 limited empirical evidence to support this hypothesis [19, but see: 24,25].

57 In this paper, we illustrate how an organism's range size can be expected to depend on  
58 both the abundance and unpredictability of resources. First, we set the theoretical back-  
59 ground necessary for the successive sections by introducing key concepts and notation. Next,  
60 we provide a review of the effects of resource abundance on range sizes while suggesting a  
61 simple and unifying hypothesis. Afterwards, we provide a review of the effects of resource  
62 stochasticity on organisms' range sizes while suggesting a second simple and unifying hypoth-  
63 esis. Subsequently, we support the two hypotheses using quantitative, simulated responses  
64 in range size to changes in resource abundance and stochasticity. Finally, we demonstrate  
65 how this framework can be used in practice to describe the movement ecology of a lowland  
66 tapir (*Tapirus terrestris*) from the Brazilian Cerrado [26].

67 **Resources as a random variable**

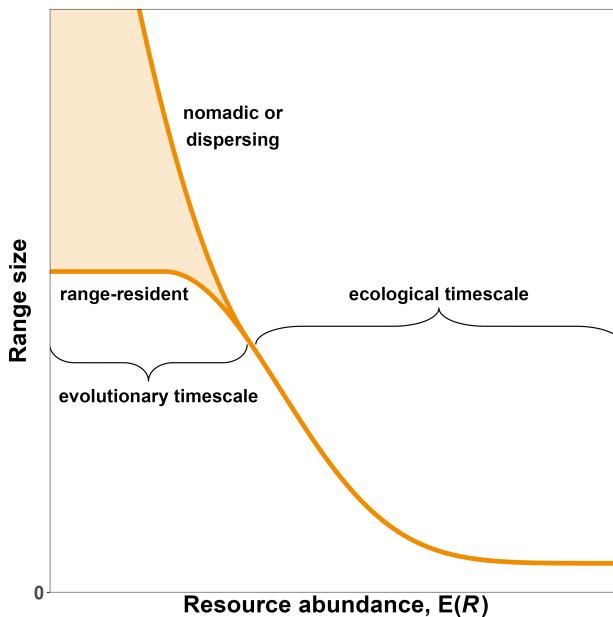
68 Resources are often unpredictable (and difficult to quantify), since they depend on various  
69 factors which cannot be accounted for easily, including climate [7,27,28], weather [28,29],  
70 competitive pressure [30,31], and differences in energetics among individuals [7] and species  
71 [32]. Thus, we can treat the amount of resources  $R$  at a given point in time ( $t$ ) and space  
72 (location vector  $\vec{u}$ ) as a random variable, denoted as  $R(t, \vec{u})$ . Treating resources as a random  
73 variable allows us to leverage techniques from probability theory and statistics, such as the  
74 expectation of a random variable (i.e., its mean) and its variance around the mean. We  
75 indicate the expected value and variance of random variable  $R$  using  $E(R)$  and  $\text{Var}(R)$ ,  
76 respectively, and we use  $\mu(t, \vec{u})$  and  $\sigma^2(t, \vec{u})$  to indicate them as functions of time ( $t$ ) and  
77 space ( $\vec{u}$ ). Appendix A defines and expands on the concepts of probability distributions,  
78 expected value, variance, and provides examples of them for gamma and beta distributions.

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

80 While organisms' needs vary greatly between taxonomic groups, some needs are essential  
81 for the growth, survival, and reproduction of most organisms. All heterotrophic organisms  
82 require sources of chemical energy (i.e., food), water, and various limiting nutrients [33–  
83 35]. As the abundance of essential resources fluctuates, motile organisms can move to new  
84 locations or 'patches' to meet their requirements [12,36], but they must also account for costs  
85 of movement [37].

86 Fig. 1 illustrates our first of two hypotheses, which is similar to that presented by  
87 [16]. When  $E(R)$  is high, we expect organisms' ranges to be relatively small and near  
88 the smallest amount of space required to survive [24,25,e.g., 38]. Like [16], we also expect  
89 organisms' range sizes to increase nonlinearly as  $E(R)$  decreases, but we highlight that  
90 organisms may adopt different behaviors at low values of  $E(R)$ . These behaviors include  
91 maximal home range expansion [30,home range size is limited by vagility, habitat structure,

92 competition, and predation, e.g., 31,39,40], migration [41–43], and nomadism [20,22,44,45].  
 93 It is unclear when organisms switch from range residency to migration or nomadism (or  
 94 vice-versa), but understanding the gradient among these types of movement is necessary  
 95 for quantifying the effect of resource abundance on organisms' range size and movement  
 96 behavior [mammals: 46, moose, *Alces alces*: 20, eagles, *Haliaeetus leucocephalus*: 21,47, lesser  
 97 flamingos, *Phoeniconaias minor*: 48]. Still, switches from range residency to nomadism (or  
 98 vice-versa) will occur over evolutionary timescales rather than over an organism's lifespan  
 99 (Fig. 1), since larger ranges require greater vagility, which, in turn, is facilitated by the  
 100 development of morphological features such as hinged joints and elongated limbs [32,49–51].



**Figure 1:** Hypothesized range size of an organism as a function of resource abundance,  $E(R)$ . We expect low values of  $E(R)$  to result in a large range, since organisms are forced to explore large areas to collect the resources they require to survive, whether they be range-resident, nomadic, or migratory. As  $E(R)$  increases, range size should decrease nonlinearly until it reaches the minimum amount of space required by the organism to survive. Note that the relationship between  $E(R)$  and range size cannot be linear because it would require range size to be negative for high values of  $E(R)$ .

101 Overall, the hypothesis that range size decreases with resource abundance,  $E(R)$ , is com-  
 102 monly accepted and well supported, but many studies assume a linear relationship [19,e.g.,  
 103 38,52–54]. This is problematic because, conceptually, the relationship between range size  
 104 and  $E(R)$  must be nonlinear, since: (1) there is an upper limit to how much space an organ-  
 105 ism is able to explore in its finite lifetime and (2) the minimum amount of space it requires

106 to survive is necessarily greater than zero [24,25,see: 55,56,57, and contrast them to the  
107 estimates based on linear models listed above]. Consequently, we suggest analysts use mod-  
108 els that account for this nonlinearity when estimating the effects of resource abundance on  
109 range size.

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

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

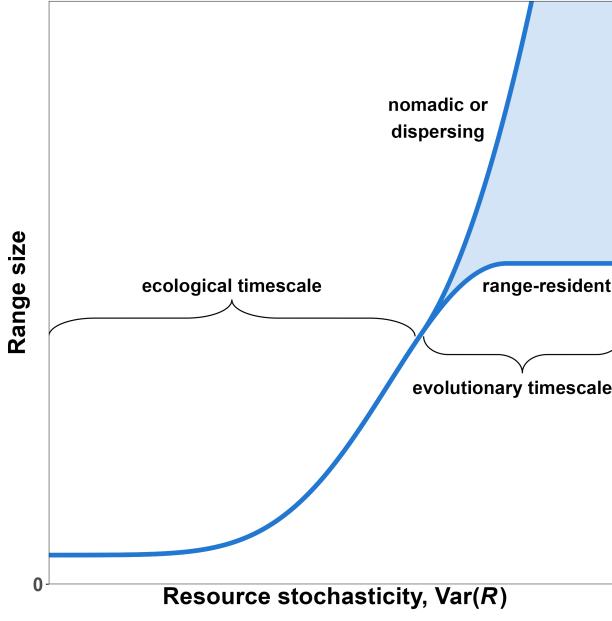
118 Recognizing changes in  $\text{Var}(R)$  helps account for the residual, fine-scale variation in  $R$   
119 after accounting for trends in the large-scale average  $R$  [e.g., variations in plant phenology  
120 between years after accounting for mean seasonal trends, see 58]. However, when both  $E(R)$   
121 and  $\text{Var}(R)$  change over time (fig. A2), disentangling changes in  $E(R)$  and  $\text{Var}(R)$  is not  
122 simple [59]. Statistically, this confound occurs because the more change one attributes to  
123  $\mu(t, \vec{u})$  (i.e., the wigglier it is), the smaller  $\sigma^2(t, \vec{u})$  becomes. Conversely, the smoother  $\mu(t, \vec{u})$   
124 is, the larger  $\sigma^2(t, \vec{u})$  becomes. Biologically, it is important because an organism's perception  
125 scale determines whether it attributes a change in  $R$  to a trend in  $E(R)$  or as a stochastic  
126 event [i.e., due to  $\text{Var}(R)$ ; see [58]]. An organism's perception of changes in  $R$  will also  
127 depend strongly on the its cognitive capacities and memory [9,60–63]. Whether an organism  
128 is able to predict trends in  $\sigma^2(t, \vec{u})$  or not, environmental variability is thought to reduce a  
129 landscape's energetic balance [23], which, in turn, decreases organisms' fitness [e.g., 10] and  
130 increases their range size. While this behavioral response occurs with both predictable and  
131 unpredictable stochasticity, extreme and rare events are more likely to have a stronger effect

132 due to their unpredictability and magnitude [64,65]. A few recent studies support these  
133 hypotheses [23,28,45,66], but many of them are limited in geographic and taxonomic scales,  
134 so the extent to which these preliminary findings can be generalized is currently unknown.  
135 Thus, there remains a need for developing a more complete understanding of how organisms'  
136 range sizes changes with environmental stochasticity.

137 Similarly to  $E(R)$ , we hypothesize  $\text{Var}(R)$  has a nonlinear effect on an organism's range  
138 size. When  $\text{Var}(R)$  is low enough that  $R$  is relatively predictable, we expect organisms to be  
139 range-resident with small home ranges, and we do not expect small changes in  $\text{Var}(R)$  to have  
140 a noticeable effect. As resources become increasingly unpredictable, we expect home range  
141 size to increase progressively faster (fig. 2) because: (1) as  $\text{Var}(R)$  increases, the chances of  
142 finding low  $R$  increase superlinearly, (2) the added movement required to search for food  
143 increases organisms' energetic requirements, and (3) stochasticity reduces an organism's abil-  
144 ity to specialize and reduce competition for  $R$  [67]. If resources remain highly unpredictable  
145 over long periods of time (e.g., multiple lifespans), organisms may evolve or develop new  
146 and consistent behaviors (e.g., nomadism) or adaptations (e.g., increased fat storage or food  
147 caching) to buffer themselves against times of unpredictably low  $R$ . Conversely, if changes  
148 in  $\sigma^2(t, \vec{u})$  are sufficiently predictable, organisms may learn to anticipate and prepare for  
149 times of greater stochasticity by pre-emptively caching food, reducing energetic needs,  
150 migrating, or relying on alternative food sources [e.g., 68].

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

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



**Figure 2:** Hypothesized range size of an organism as a function of resource stochasticity,  $\text{Var}(R)$ . We expect low values of  $\text{Var}(R)$  to result in small home-ranges, since organisms are able to depend on relatively predictable resources. As  $\text{Var}(R)$  increases, range size should increase nonlinearly, whether this results in an expansion of the home range (in the case of range-resident organisms) or a switch to a larger range via dispersal, nomadism, or migration. Note that the relationship between  $\text{Var}(R)$  and range size cannot be linear because it would require range size to be negative for low values of  $\text{Var}(R)$ .

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

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

162 To support our hypotheses of how organisms' range sizes are affected by  $E(R)$ ,  $\text{Var}(R)$ , and  
 163 the interaction effect of  $E(R)$  and  $\text{Var}(R)$ , we present the results from a series of quantitative  
 164 simulations. To start, we used the `ctmm` package [69] for R [70] to generate 200 tracks  
 165 (see Appendix B for sensitivity analyses) from an Integrated Ornstein-Uhlenbeck movement  
 166 model [IOU model, see 71]. The IOU model's correlated velocity produced realistic tracks  
 167 with directional persistence, but, unlike Ornstein-Uhlenbeck (OU) and Ornstein-Uhlenbeck  
 168 Foraging (OUF) models, IOU models do not produce spatially stationary movement, so the  
 169 organism is not range-resident. Consequently, each track is spatially unrestricted and can  
 170 be interpreted as purely exploratory or memoryless movement.

171     Each of the 200 tracks were placed on a grid with common starting point  $\langle 0, 0 \rangle$  (fig. B1).  
172    Each time the simulated individual moved to a new cell, it collected  $R$  resources sampled  
173    from a Gamma distribution. The mean and variance of the distribution were defined by a  
174    series of deterministic functions  $\mu(t)$  and  $\sigma^2(t)$  (orange and blue lines in fig. 3). The value  
175    of  $t$  was constant within each set of 200 tracks, so the distribution  $R$  was sampled from  
176    was independent of both the organism's location and its time spent moving. Tracks were  
177    truncated once the organism reached satiety, and the organism was given enough time to  
178    return to  $\langle 0, 0 \rangle$  independently from the following track (section 2.1 of Appendix B). Finally,  
179    we fit an OUF movement model [72] to the set of tracks to calculate the 95% Gaussian  
180    home-range size using the formula

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

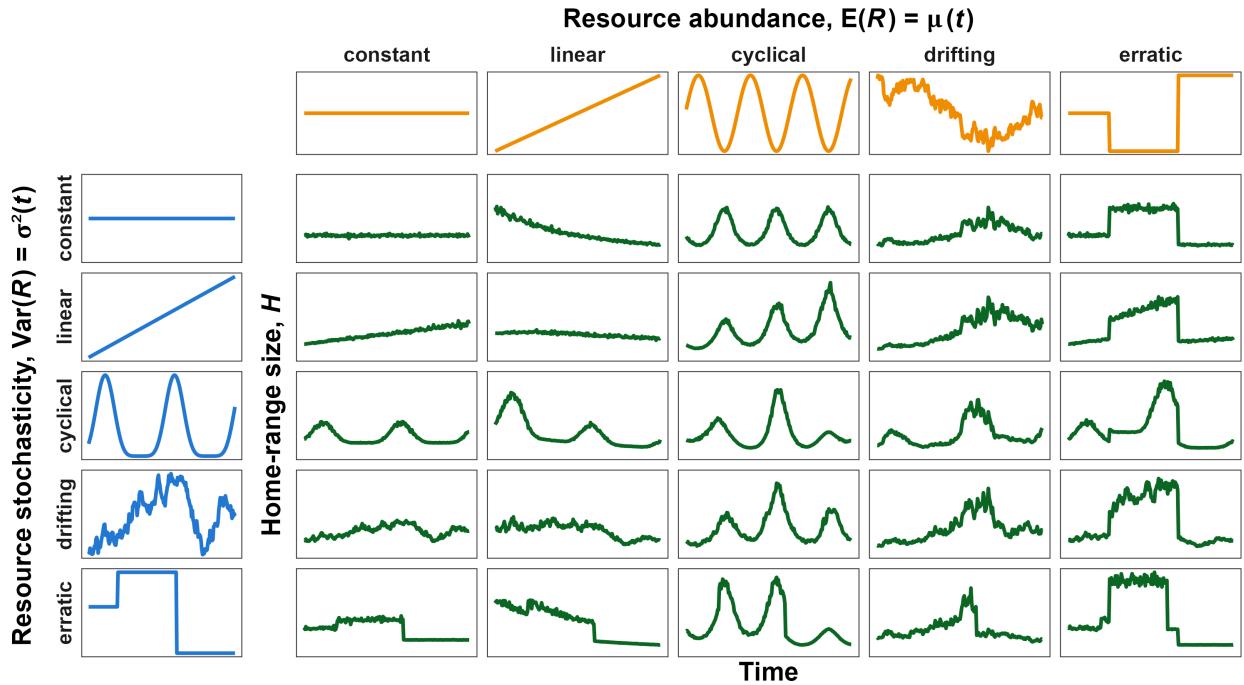
181    where  $\hat{\zeta}^2$  is the positional variance estimated by the movement model.

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

- 185    1) Environments are homogeneous for a given  $t$ . Given  $t$ ,  $E(R) = \mu(t)$  and  $\text{Var}(R) = \sigma^2(t)$   
186       are constant over space and within each set of 200 tracks, but  $R$  is random and follows  
187       a  $\Gamma(\mu(t), \sigma^2(t))$  distribution.
- 188    2) There are no external pressures on the simulated organism. Resources do not deplete,  
189       and there is no competition nor predator avoidance.
- 190    3) The organism has a fixed daily energetic requirement that is independent of movement  
191       rates, and it cannot alter its metabolism or physiology. Additionally, the organism  
192       does not have energetic reserves, so excess resources cannot be carried over to the next  
193       track or  $t$ .
- 194    4) The organism is range-resident and can only respond to changes in  $E(R)$  and  $\text{Var}(R)$

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

203 Additional information is provided in Appendix B, including the directed acyclical graph  
204 [see fig. B6 and 73] we used to infer causal the mechanisms of changes in  $H$  and estimate the  
205 direct effects of  $E(R)$  and  $\text{Var}(R)$  on  $H$  (contrast the graph with fig. C3 and the empirical  
206 case study below).



**Figure 3:** Simulated home-range sizes,  $H$ , of an organism living in habitats where the mean and variance in resources are constant, linearly increasing, cyclical, drifting, or erratic over time (but 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.

207 Fig. 3 shows how simulated home-range size,  $H$ , responded to changes in  $\mu(t)$  and  $\sigma^2(t)$

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

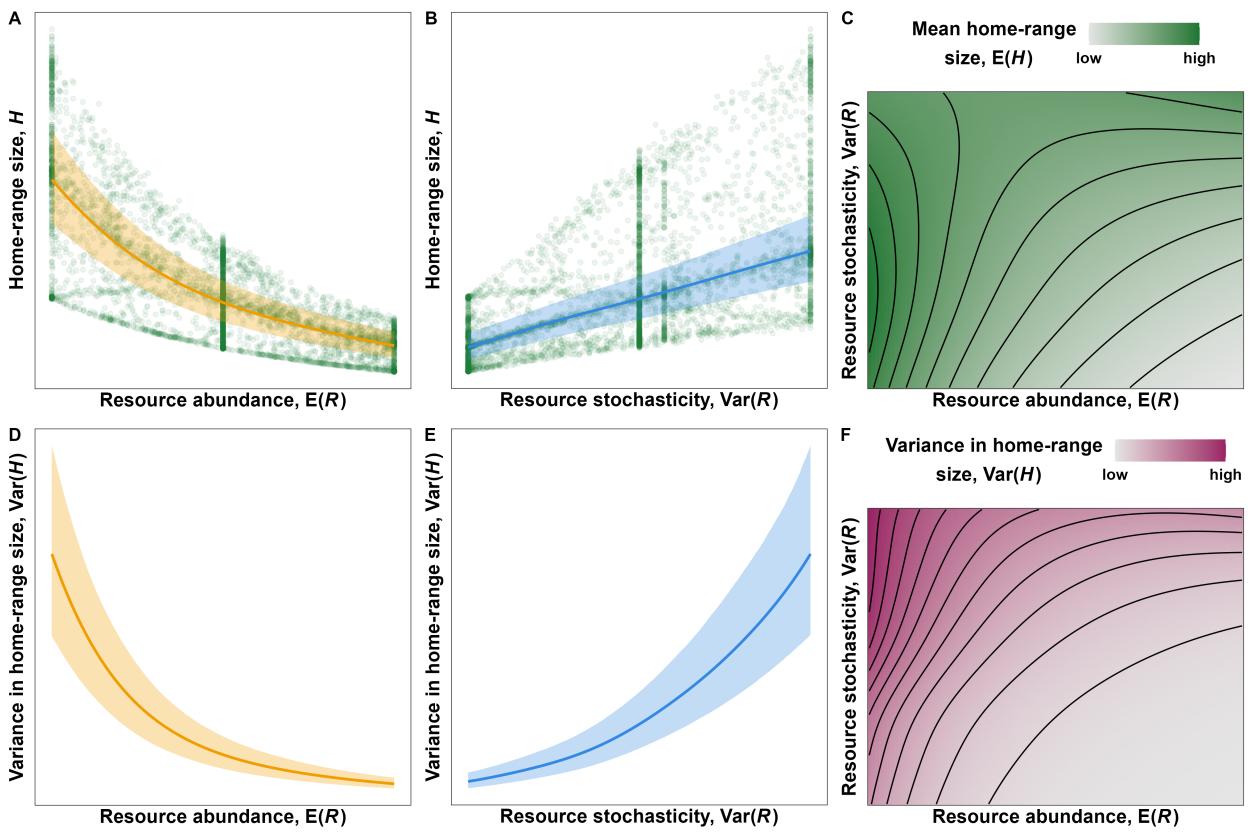
214 The leftmost column of fig. 3 (constant  $E(R)$ ) illustrates the effects of  $\text{Var}(R)$  on  $H$   
215 while  $E(R)$  remains constant. Overall, both mean  $H$  and the variance around it increase  
216 with  $\sigma^2(t)$  (most visible with constant  $E(R)$  and linear  $\text{Var}(R)$ ).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

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

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

when  $E(R)$  is high the effect of  $\text{Var}(R)$  on  $E(H)$  is exponential. Similarly,  $E(H)$  decreases exponentially with  $E(R)$  except when  $\text{Var}(R)$  is very high.

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



**Figure 4:** Effects of  $E(R)$  and  $\text{Var}(R)$  on the mean (A-C) and variance (D-F) in simulated home-range size with 95% Bayesian credible intervals. While the estimated marginal effect of  $\text{Var}(R)$  on  $E(H)$  is sublinear (panel B), the effect of  $\text{Var}(R)$  is superlinear for high values of  $E(R)$  (panel C). The relationships were estimated using a Generalized Additive Model for Location and Scale with a Gamma location-scale family of distributions (`mgcv::gammals`). Credible intervals were calculated using 10,000 samples from the posterior distribution while assuming multivariate Gaussian coefficients. Additional details on the model structure are provided in Appendix B.

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

245 The simulations in the section above support the hypotheses we presented in the introduction,  
246 but they are based on assumptions that are often not met in real natural environments.  
247 Organisms live in spatiotemporally heterogeneous and dynamic environments that promote  
248 the use of perceptual ranges, navigation, and memory. Together, these abilities result in  
249 selective space use that depends on resource availability [11] and resource depletion [12].

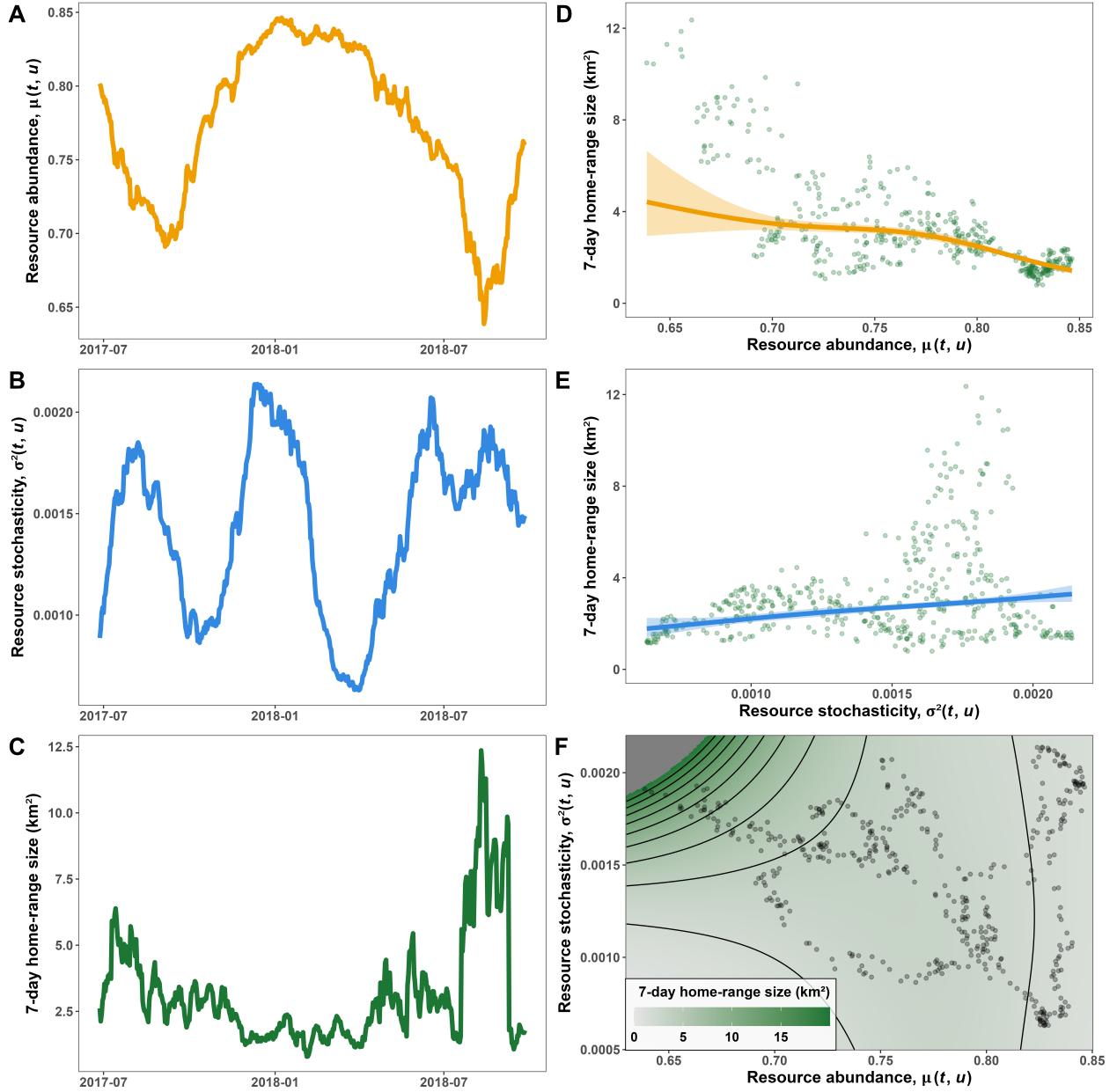
250 In this section, we test the hypotheses using empirical tracking data on a lowland tapir  
251 from the Brazilian Cerrado along with empirical estimates of  $E(R)$  and  $\text{Var}(R)$ . We measure  
252  $R$  using Normalized Difference Vegetation Index [NDVI, see 74], a remote-sensed measure  
253 of landscape greenness, as a proxy for forage abundance. Appendix C contains additional  
254 information on how we modeled NDVI and the tapir’s movement using continuous-time  
255 movement models [69,75] and autocorrelated kernel density estimation [76–78].

256 Fig. 5 illustrates how a tapir in the Brazilian Cerrado adapts its 7-day home-range size to  
257 spatiotemporal changes in  $\mu(t, \vec{u})$  and  $\sigma^2(t, \vec{u})$  [telemetry data from the individual labelled as  
258 “Anna” in the dataset from 26]. Panels A and B show the changes in seven-day average mean  
259 and variance in NDVI, respectively, experienced by the tapir during the tracking period. The  
260 mean and variance in NDVI were estimated using a Generalized Additive Model for Location  
261 and Scale [GAMLS, 79] with a Beta family of distributions (NDVI values ranged from 0.3534  
262 to 0.9475). Panel C shows the changes in the tapir’s 7-day home range over time. Note how  
263 the tapir uses more space during periods of lower NDVI (e.g., August 2017) and less space  
264 during periods with high NDVI (January 2018). Additionally, when resources are scarce  
265 and highly unpredictable (August 2018), the tapir uses up to 5 times more space than when  
266 resources are abundant and predictable (e.g., January 2018). Finally, panels D and E show  
267 the estimated (marginal) effects of  $\mu(t, \vec{u})$  and  $\sigma^2(t, \vec{u})$  on the tapir’s 7-day home-range  
268 size. Since  $\mu(t, \vec{u})$  and  $\sigma^2(t, \vec{u})$  are correlated (panel F) and spatiotemporally autocorrelated  
269 (panels A, B, and F), the effects of  $R$  on  $H$  should be modeled carefully. To avoid over-fitting

the model, we constrained the smooth effects of  $\mu(t, \vec{u})$  and  $\sigma^2(t, \vec{u})$  and their interaction effect to a small basis size ( $k = 3$ ). Additional information is provided in appendix C. The results presented in panels D-F of fig. 5 match our findings from the simulations: The tapir's 7-day home range decreases with  $\mu(t, \vec{u})$  and increases with  $\sigma^2(t, \vec{u})$ , and the effect of  $\mu(t, \vec{u})$  depends on  $\sigma^2(t, \vec{u})$ , and vice-versa. Alone,  $\mu(t, \vec{u})$  and  $\sigma^2(t, \vec{u})$  cause the tapir to double her home range (panels D and E), but together they result in an approximate 15-fold change in home-range size (observed range: 0.8 to 12.4 km<sup>2</sup>; see panel F). Additionally, note how high NDVI values ( $> 0.8$ ) cause  $\sigma^2(t, \vec{u})$  to have little to no effect on home-range size, as indicated by the vertical contour line in panel F.

## Discussion

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



**Figure 5:** Effects of  $\mu(t, \vec{u})$  and  $\sigma^2(t, \vec{u})$  on the home-range size of a lowland tapir (*Tapirus terrestris*). (A) Trends in resource abundance over time,  $\mu(t, \vec{u})$ , estimated as the average mean NDVI at the locations visited by the tapir during a seven-day period. (B) Variance in resources over time,  $\sigma^2(t, \vec{u})$ , estimated as the average variance in NDVI at the locations visited by the tapir during a seven-day period. (C) Seven-day 95% home range estimated using Autocorrelated Kernel Density Estimation. (D, E) Estimated marginal effects of  $\mu(t, \vec{u})$  and  $\sigma^2(t, \vec{u})$  on home-range size. The model accounted for the marginal effects of  $\mu(t, \vec{u})$  and  $\sigma^2(t, \vec{u})$  and their interaction effect. (F) Estimated home-range size in response to changes in both  $\mu(t, \vec{u})$  and  $\sigma^2(t, \vec{u})$ . Note how the effect of  $\sigma^2(t, \vec{u})$  is more pronounced when  $\mu(t, \vec{u})$  is low. See Appendix C for additional information. The tapir movement data corresponds to the individual named “Anna” from the Cerrado sample of Medici *et al.* (2022).

296 the shape of a Gamma distribution as much if  $E(R)$  is low (fig. B3). Secondly, and perhaps  
297 more interestingly, the simulation approach does not account for real-world adaptations to  
298  $E(R)$  and  $\text{Var}(R)$  such as selective space use, which we account for in the empirical approach.  
299 Below we discuss the strengths and limitations of each approach.

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

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

310 Deviations from the simulations offer a means of detecting when the underlying assump-  
311 tions are inappropriate and how additional factors may affect organisms' responses to changes  
312 in  $E(R)$  and  $\text{Var}(R)$ . For example, energetic costs of movement are often non-negligible and  
313 depend on organism size [37], movement speed [37], and ambient temperature [1,80]. In addi-  
314 tion, an organism may alter its movement behavior, physiology, and energetic needs to buffer  
315 itself against changes in  $E(R)$  and  $\text{Var}(R)$  by using space selectively [66,81–83] and adapting  
316 their behavior and physiology over time [15,67]. Before or during periods of scarcity, organ-  
317 isms may cache resources [84], build up fat reserves [42], enter states of dormancy [85–87],  
318 or even pause fetal growth [7]. However, organisms may be unable to respond to changes  
319 in  $E(R)$  and  $\text{Var}(R)$  optimally due to various reasons, including limited perceptive range  
320 [59], lack of experience [9,44,61–63,88], avoidance of competitors and predators [11,89], or a  
321 physiology that is not amenable to things like hibernation or fat storage. Thus organisms

322 may relocate their range to a sub-optimal location [30,31,90,91], which may exacerbate the  
323 effects of  $E(R)$  and  $\text{Var}(R)$  on both mean range size and the variance around it.

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

325 There are two main advantages of taking an empirical approach. Firstly, modeling real-world  
326 animal movement data can produce scale-appropriate and easily interpretable estimates.  
327 Secondly, empirical models directly quantify the effects of  $E(R)$ ,  $\text{Var}(R)$ , and confounding  
328 variables without having to design complex and time-consuming simulations. However, it is  
329 not always possible to quantify confounding variables. For example, while there may be some  
330 appropriate proxies of competition, such as density of competitors, these variables may be  
331 hard to quantify, and they may not account for the confounding effects appropriately (i.e.,  
332 the presence of competitors may not reflect competitive pressure). This is problematic if  
333 one is interested in estimating the direct causal effect of  $E(R)$  and  $\text{Var}(R)$ , which requires  
334 removing any non-negligible confounding effects [73].

335 Similarly, if  $R$  is often non-measurable. Proxies of  $R$ , such as NDVI [74], which may  
336 introduce complexities. While  $R$  and NDVI are correlated for many species [42,43,88,e.g.,  
337 92,93,94], the relationship between the two can be weak [95], satellite-dependent [96], and  
338 nonlinear [96,97]. This complexity can introduce two sources of bias: ecosystem-level biases  
339 (indicated as  $Z$  in the directed acyclical graph in fig. C3) and satellite-level confounding  
340 variables ( $S$  in fig. C3). Examples of ecosystem-level biases are the effects of competition,  
341 predation, habitat connectivity, and movement costs, all of which can depend on habitat  
342 quality, and, consequently, be correlated nonlinearly to  $R$  and NDVI [32,98]. Resource-rich  
343 patches can attract larger amounts of competitors [11] and predators [18], which may, in  
344 turn, increase pressures from competition and predation [12,36]. However, such pressures  
345 may result in both an expansion of the range [32,98] or a contraction, since larger ranges can  
346 be harder to defend and result in higher movement costs [32,99] and encounter rates [100].  
347 Satellite-level confounds include information loss due to coarse spatiotemporal resolution

[96,97], satellite-level error [96,97,101], and other limitations of remote sensing (e.g., inability to quantify specific resources or small-scale resource depletion). However, nonlinear models such as Generalized Additive Models [102] can help account for preferences for intermediate values of remotely-sensed  $R$  [e.g., young grass rather than mature grasslands, see 96].

## Conclusion

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

Recent advances in computational power have greatly increased analysts' ability to fit computationally demanding models [103,104] that allow biologists to move beyond only considering changes in mean conditions. By accounting for changes in stochasticity, we can start developing a more comprehensive understanding of how organisms adapt to the dynamic environments organisms live in, including recent changes in climate [105] and increases in the frequency and intensity of extreme events [64,65,106–108].

## Acknowledgements

We would like to thank Dr. Simon Wood for providing code to fit a Beta location-scale GAM despite not being involved directly with the project. Additionally, we thank all those who provided feedback on all posters, presentation, and writings related to this project. In particular, we thank all those who provided feedback on the manuscript and appendices despite not being authors, namely, in alphabetical order by first name: Aimee Chhen, Jessa Marley, Kim Hinz, Lauren Mills, Sarah Wyse, and Dr. Simon Wood. This work was supported by the NSERC Discovery Grant RGPIN-2021-02758 to MJN and funds from the University

<sup>372</sup> of British Columbia Okanagan, the Canadian Foundation for Innovation, Mitacs, and BC  
<sup>373</sup> Parks.

<sup>374</sup> **Code and data availability**

<sup>375</sup> All code and data used for this manuscript is available on GitHub at <https://github.com/>  
<sup>376</sup> QuantitativeEcologyLab/hr-resource-stoch, with the exception of the tapir data, which is  
<sup>377</sup> available at <https://github.com/StefanoMezzini/tapirs>.

<sup>378</sup> **Conflict of interest**

<sup>379</sup> The authors declare there are no conflicts of interest.

<sup>380</sup> **References**

- <sup>381</sup> 1. Hou R, Chapman CA, Jay O, Guo S, Li B, Raubenheimer D. Cold and hungry: Combined  
<sup>382</sup> effects of low temperature and resource scarcity on an edge-of-range temperate primate,  
<sup>383</sup> the golden snub-nose monkey. *Ecography* [Internet]. 2020 [cited 2022 Oct 3];43:1672–82.  
<sup>384</sup> Available from: <https://onlinelibrary.wiley.com/doi/10.1111/ecog.05295>
- <sup>385</sup> 2. Le Bot T, Lescroël A, Fort J, Péron C, Gimenez O, Provost P, et al. Fishery discards  
<sup>386</sup> do not compensate natural prey shortage in northern gannets from the english channel.  
<sup>387</sup> *Biological Conservation* [Internet]. 2019 [cited 2022 Oct 3];236:375–84. Available from:  
<sup>388</sup> <https://linkinghub.elsevier.com/retrieve/pii/S0006320718310930>
- <sup>389</sup> 3. Dai Pra R, Mohr SM, Merriman DK, Bagriantsev SN, Gracheva EO. Ground squir-  
<sup>390</sup>rels initiate sexual maturation during hibernation. *Current Biology* [Internet]. 2022 [cited  
<sup>391</sup> 2022 Sep 2];32:1822–1828.e4. Available from: <https://linkinghub.elsevier.com/retrieve/pii/>  
<sup>392</sup> S0960982222002548
- <sup>393</sup> 4. Rocha JL, Godinho R, Brito JC, Nielsen R. Life in deserts: The genetic basis of  
<sup>394</sup> mammalian desert adaptation. *Trends in Ecology & Evolution* [Internet]. 2021 [cited  
<sup>395</sup> 2022 Sep 2];36:637–50. Available from: <https://linkinghub.elsevier.com/retrieve/pii/>  
<sup>396</sup> S0169534721000744
- <sup>397</sup> 5. Wessling EG, Deschner T, Mundry R, Pruetz JD, Wittig RM, Kühl HS. Seasonal varia-  
<sup>398</sup>tion in physiology challenges the notion of chimpanzees (*pan troglodytes verus*) as a forest-  
<sup>399</sup>adapted species. *Front Ecol Evol* [Internet]. 2018 [cited 2022 Sep 2];6:60. Available from:  
<sup>400</sup> <http://journal.frontiersin.org/article/10.3389/fevo.2018.00060/full>

- 401 6. Stefanescu C, Ubach A, Wiklund C. Timing of mating, reproductive status and resource  
402 availability in relation to migration in the painted lady butterfly. *Animal Behaviour* [Internet].  
403 2021 [cited 2022 Sep 2];172:145–53. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S0003347220303742>
- 405 7. Schmidt NM, Grøndahl C, Evans AL, Desforges J-P, Blake J, Hansen LH, et al. On the in-  
406 terplay between hypothermia and reproduction in a high arctic ungulate. *Sci Rep* [Internet].  
407 2020 [cited 2022 Sep 2];10:1514. Available from: <http://www.nature.com/articles/s41598-020-58298-8>
- 409 8. Douglas DJT, Pearce-Higgins JW. Relative importance of prey abundance and habitat  
410 structure as drivers of shorebird breeding success and abundance: Drivers of shorebird breed-  
411 ing success and abundance. *Anim Conserv* [Internet]. 2014 [cited 2022 Nov 8];17:535–43.  
412 Available from: <https://onlinelibrary.wiley.com/doi/10.1111/acv.12119>
- 413 9. Foley C, Pettorelli N, Foley L. Severe drought and calf survival in elephants. *Bi-  
414 ology Letters* [Internet]. 2008 [cited 2020 Feb 12];4:541–4. Available from: <https://royalsocietypublishing.org/doi/10.1098/rsbl.2008.0370>
- 416 10. Berger J, Hartway C, Gruzdev A, Johnson M. Climate degradation and extreme icing  
417 events constrain life in cold-adapted mammals. *Scientific Reports* [Internet]. 2018 [cited  
418 2020 Jan 24];8:1156. Available from: <http://www.nature.com/articles/s41598-018-19416-9>
- 419 11. Kacelnik A, Krebs JR, Bernstein C. The ideal free distribution and predator-prey popu-  
420 lations. *Trends in Ecology & Evolution* [Internet]. 1992 [cited 2024 Jan 31];7:50–5. Available  
421 from: <https://linkinghub.elsevier.com/retrieve/pii/016953479290106L>

- <sup>422</sup> 12. Charnov EL. Optimal foraging, the marginal value theorem. *Theoretical Population*  
<sup>423</sup> *Biology* [Internet]. 1976 [cited 2024 Jan 31];9:129–36. Available from: <https://linkinghub.elsevier.com/retrieve/pii/004058097690040X>
- <sup>425</sup> 13. Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, et al. A movement  
<sup>426</sup> ecology paradigm for unifying organismal movement research. *Proc Natl Acad Sci USA*  
<sup>427</sup> [Internet]. 2008 [cited 2022 Mar 9];105:19052–9. Available from: <https://pnas.org/doi/full/10.1073/pnas.0800375105>
- <sup>429</sup> 14. Burt WH. Territoriality and home range concepts as applied to mammals. *Journal of*  
<sup>430</sup> *Mammalogy* [Internet]. 1943 [cited 2022 Jan 31];24:346. Available from: <https://academic.oup.com/jmammal/article-lookup/doi/10.2307/1374834>
- <sup>432</sup> 15. Southwood TRE. Habitat, the templet for ecological strategies? *The Journal of Animal*  
<sup>433</sup> *Ecology* [Internet]. 1977 [cited 2022 Feb 4];46:336. Available from: <https://www.jstor.org/stable/3817?origin=crossref>
- <sup>435</sup> 16. Harestad AS, Bunnel FL. Home range and body weight—a reevaluation. *Ecology* [In-  
<sup>436</sup> ternet]. 1979 [cited 2022 Sep 5];60:389–402. Available from: <http://doi.wiley.com/10.2307/1937667>
- <sup>438</sup> 17. Stephens DW, Charnov EL. Optimal foraging: Some simple stochastic models. *Behav*  
<sup>439</sup> *Ecol Sociobiol* [Internet]. 1982 [cited 2024 Jan 31];10:251–63. Available from: <http://link.springer.com/10.1007/BF00302814>
- <sup>441</sup> 18. Duncan C, Nilssen EB, Linnell JDC, Pettorelli N. Life-history attributes and resource  
<sup>442</sup> dynamics determine intraspecific home-range sizes in carnivora. *Remote Sens Ecol Con-*

- <sup>443</sup> serv [Internet]. 2015 [cited 2024 May 29];1:39–50. Available from: <https://zslpublications.onlinelibrary.wiley.com/doi/10.1002/rse2.6>
- <sup>444</sup> 19. Rizzuto M, Leroux SJ, Vander Wal E, Richmond IC, Heckford TR, Balluffi-Fry J, et al. Forage stoichiometry predicts the home range size of a small terrestrial herbivore. *Oecologia* [Internet]. 2021 [cited 2022 Mar 2];197:327–38. Available from: <https://link.springer.com/10.1007/s00442-021-04965-0>
- <sup>445</sup> 20. Singh NJ, Börger L, Dettki H, Bunnefeld N, Ericsson G. From migration to nomadism: Movement variability in a northern ungulate across its latitudinal range. *Ecological Applications* [Internet]. 2012 [cited 2022 Nov 17];22:2007–20. Available from: <http://doi.wiley.com/10.1890/12-0245.1>
- <sup>453</sup> 21. Wheat RE, Lewis SB, Wang Y, Levi T, Wilmers CC. To migrate, stay put, or wander? Varied movement strategies in bald eagles (*haliaeetus leucocephalus*). *Mov Ecol* [Internet]. 2017 [cited 2022 Oct 17];5:9. Available from: <http://movementecologyjournal.biomedcentral.com/articles/10.1186/s40462-017-0102-4>
- <sup>457</sup> 22. Teitelbaum CS, Mueller T. Beyond migration: Causes and consequences of nomadic animal movements. *Trends in Ecology & Evolution* [Internet]. 2019 [cited 2022 Feb 1];34:569–81. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S0169534719300527>
- <sup>460</sup> 23. Chevin L-M, Lande R, Mace GM. Adaptation, plasticity, and extinction in a changing environment: Towards a predictive theory. Kingsolver JG, editor. *PLoS Biology* [Internet]. 2010 [cited 2020 Nov 11];8:e1000357. Available from: <https://dx.plos.org/10.1371/journal.pbio.1000357>

- <sup>464</sup> 24. Herfindal I, Linnell JDC, Odden J, Nilsen EB, Andersen R. Prey density, environmental  
<sup>465</sup> productivity and home-range size in the eurasian lynx (*lynx lynx*). *Journal of Zoology*  
<sup>466</sup> [Internet]. 2005 [cited 2022 Sep 23];265:63–71. Available from: <https://onlinelibrary.wiley.com/doi/10.1017/S0952836904006053>
- <sup>468</sup> 25. Nilsen EB, Herfindal I, Linnell JDC. Can intra-specific variation in carnivore home-range  
<sup>469</sup> size be explained using remote-sensing estimates of environmental productivity? *Écoscience*  
<sup>470</sup> [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>
- <sup>472</sup> 26. Medici EP, Mezzini S, Fleming CH, Calabrese JM, Noonan MJ. Movement ecology  
<sup>473</sup> of vulnerable lowland tapirs between areas of varying human disturbance. *Mov Ecol* [In-  
<sup>474</sup> ternet]. 2022 [cited 2022 Mar 14];10:14. Available from: <https://movementecologyjournal.biomedcentral.com/articles/10.1186/s40462-022-00313-w>
- <sup>476</sup> 27. Lindstedt SL, Boyce MS. Seasonality, fasting endurance, and body size in mammals.  
<sup>477</sup> *The American Naturalist* [Internet]. 1985 [cited 2022 Feb 4];125:873–8. Available from:  
<sup>478</sup> <https://www.journals.uchicago.edu/doi/10.1086/284385>
- <sup>479</sup> 28. Morellet N, Bonenfant C, Börger L, Ossi F, Cagnacci F, Heurich M, et al. Seasonality,  
<sup>480</sup> weather and climate affect home range size in roe deer across a wide latitudinal gradient  
<sup>481</sup> within europe. Coulson T, editor. *Journal of Animal Ecology* [Internet]. 2013 [cited 2020  
<sup>482</sup> Nov 11];82:1326–39. Available from: <http://doi.wiley.com/10.1111/1365-2656.12105>
- <sup>483</sup> 29. Fjelldal MA, Wright J, Stawski C. Nightly torpor use in response to weather conditions  
<sup>484</sup> and individual state in an insectivorous bat. *Oecologia* [Internet]. 2021 [cited 2022 Oct  
<sup>485</sup> 3];197:129–42. Available from: <https://link.springer.com/10.1007/s00442-021-05022-6>

- 486 30. Tórrez-Herrera LL, Davis GH, Crofoot MC. Do monkeys avoid areas of home range  
487 overlap because they are dangerous? A test of the risk hypothesis in white-faced capuchin  
488 monkeys (*cebus capucinus*). *Int J Primatol* [Internet]. 2020 [cited 2022 Mar 9];41:246–64.  
489 Available from: <http://link.springer.com/10.1007/s10764-019-00110-0>
- 490 31. Rich LN, Mitchell MS, Gude JA, Sime CA. Anthropogenic mortality, intraspecific com-  
491 petition, and prey availability influence territory sizes of wolves in montana. *J Mammal*  
492 [Internet]. 2012 [cited 2022 Mar 10];93:722–31. Available from: <https://academic.oup.com/jmammal/article-lookup/doi/10.1644/11-MAMM-A-079.2>
- 494 32. Jetz W, Carbone C, Fulford J, Brown JH. The scaling of animal space use. *Science*  
495 [Internet]. 2004 [cited 2022 Mar 3];306:266–8. Available from: <https://www.science.org/doi/10.1126/science.1102138>
- 497 33. Harvey PH, Clutton-Brock TH. Primate home-range size and metabolic needs. *Behav*  
498 *Ecol Sociobiol* [Internet]. 1981 [cited 2022 Nov 12];8:151–5. Available from: <http://link.springer.com/10.1007/BF00300828>
- 500 34. Baldwin R, Bywater A. Nutritional energetics of animals. *Annual review of nutrition*.  
501 1984;4:101–14.
- 502 35. Reich PB. Body size, geometry, longevity and metabolism: Do plant leaves behave like  
503 animal bodies? *Trends in Ecology & Evolution* [Internet]. 2001 [cited 2022 Oct 17];16:674–  
504 80. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S0169534701023060>
- 505 36. Brown JS, Laundre JW, Gurung M. The ecology of fear: Optimal foraging, game  
506 theory, and trophic interactions. *Journal of Mammalogy* [Internet]. 1999 [cited 2024 Jan

507 31];80:385–99. Available from: <https://academic.oup.com/jmammal/article-lookup/doi/10.2307/1383287>

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

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

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

522 40. Berger-Tal O, Saltz D. Invisible barriers: Anthropogenic impacts on inter- and  
523 intra-specific interactions as drivers of landscape-independent fragmentation. Phil  
524 Trans R Soc B [Internet]. 2019 [cited 2022 Aug 11];374:20180049. Available from:  
525 <https://royalsocietypublishing.org/doi/10.1098/rstb.2018.0049>

526 41. Samarra FIP, Tavares SB, Béesau J, Deecke VB, Fennell A, Miller PJO, et al. Movements  
527 and site fidelity of killer whales (*orcinus orca*) relative to seasonal and long-term shifts in  
528 herring (*clupea harengus*) distribution. Mar Biol [Internet]. 2017 [cited 2022 Nov 7];164:159.

- 529 Available from: <http://link.springer.com/10.1007/s00227-017-3187-9>
- 530 42. Middleton AD, Merkle JA, McWhirter DE, Cook JG, Cook RC, White PJ, et al. Green-  
531 wave surfing increases fat gain in a migratory ungulate. *Oikos* [Internet]. 2018 [cited 2022  
532 Sep 2];127:1060–8. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/oik.05227>
- 533 43. Geremia C, Merkle JA, Eacker DR, Wallen RL, White PJ, Hebblewhite M, et al. Mi-  
534 grating bison engineer the green wave. *Proc Natl Acad Sci USA* [Internet]. 2019 [cited  
535 2022 Mar 2];116:25707–13. Available from: <http://www.pnas.org/lookup/doi/10.1073/pnas.1913783116>
- 536
- 537 44. Polansky L, Kilian W, Wittemyer G. Elucidating the significance of spatial memory  
538 on movement decisions by african savannah elephants using state-space models. *Proc  
539 R Soc B* [Internet]. 2015 [cited 2022 Feb 10];282:20143042. Available from: <https://royalsocietypublishing.org/doi/10.1098/rspb.2014.3042>
- 540
- 541 45. Nandintsetseg D, Bracis C, Leimgruber P, Kaczensky P, Buuveibaatar B, Lkhagvasuren  
542 B, et al. Variability in nomadism: Environmental gradients modulate the movement behav-  
543 iors of dryland ungulates. *Ecosphere* [Internet]. 2019 [cited 2020 Nov 11];10. Available from:  
544 <https://onlinelibrary.wiley.com/doi/abs/10.1002/ecs2.2924>
- 545
- 546 46. Teitelbaum CS, Fagan WF, Fleming CH, Dressler G, Calabrese JM, Leimgruber P, et  
547 al. How far to go? Determinants of migration distance in land mammals. *Festa-Bianchet*  
548 M, editor. *Ecol Lett* [Internet]. 2015 [cited 2022 Sep 23];18:545–52. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/ele.12435>
- 549 47. Poessel SA, Woodbridge B, Smith BW, Murphy RK, Bedrosian BE, Bell DA, et al.

- 550 Interpreting long-distance movements of non-migratory golden eagles: Prospecting and  
551 nomadism? *Ecosphere* [Internet]. 2022 [cited 2022 Nov 18];13. Available from: <https://onlinelibrary.wiley.com/doi/10.1002/ecs2.4072>
- 553 48. Pretorius MD, Leeuwner L, Tate GJ, Botha A, Michael MD, Durgaprasad K, et al.  
554 Movement patterns of lesser flamingos *phoeniconaias minor* : Nomadism or partial migra-  
555 tion? *Wildlife Biology* [Internet]. 2020 [cited 2022 Nov 17];2020:1–11. Available from:  
556 <https://onlinelibrary.wiley.com/doi/10.2981/wlb.00728>
- 557 49. Hirt MR, Jetz W, Rall BC, Brose U. A general scaling law reveals why the largest  
558 animals are not the fastest. *Nat Ecol Evol* [Internet]. 2017 [cited 2022 Mar 11];1:1116–22.  
559 Available from: <http://www.nature.com/articles/s41559-017-0241-4>
- 560 50. Andersson K. Elbow-joint morphology as a guide to forearm function and foraging  
561 behaviour in mammalian carnivores. *Zoological Journal of the Linnean Society* [Internet].  
562 2004 [cited 2023 Jul 6];142:91–104. Available from: <https://academic.oup.com/zoolinnean/article-lookup/doi/10.1111/j.1096-3642.2004.00129.x>
- 564 51. Samuels JX, Meachen JA, Sakai SA. Postcranial morphology and the locomotor habits  
565 of living and extinct carnivorans. *J Morphol* [Internet]. 2013 [cited 2023 Jul 6];274:121–46.  
566 Available from: <https://onlinelibrary.wiley.com/doi/10.1002/jmor.20077>
- 567 52. Bista D, Baxter GS, Hudson NJ, Lama ST, Murray PJ. Effect of disturbances and  
568 habitat fragmentation on an arboreal habitat specialist mammal using GPS telemetry: A  
569 case of the red panda. *Landsc Ecol* [Internet]. 2022 [cited 2022 Aug 24];37:795–809. Available  
570 from: <https://link.springer.com/10.1007/s10980-021-01357-w>

- 571 53. Bradsworth N, White JG, Rendall AR, Carter N, Whisson DA, Cooke R. Using thresh-  
572 olds to determine priorities for apex predator conservation in an urban landscape. Land-  
573 scape and Urban Planning [Internet]. 2022 [cited 2022 Oct 18];228:104559. Available from:  
574 <https://github.com/ropensci/MODIStsp>
- 575 54. McClintic LF, Taylor JD, Jones JC, Singleton RD, Wang G. Effects of spatiotemporal  
576 resource heterogeneity on home range size of american beaver. J Zool [Internet]. 2014 [cited  
577 2022 Nov 12];293:134–41. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/jzo.12128>
- 579 55. Lucherini M, Lovari S. Habitat richness affects home range size in the red fox *vulpes*  
580 *vulpes*. Behavioural Processes [Internet]. 1996 [cited 2021 Nov 29];36:103–5. Available from:  
581 <https://linkinghub.elsevier.com/retrieve/pii/0376635795000186>
- 582 56. Simcharoen A, Savini T, Gale GA, Simcharoen S, Duangchantrasiri S, Pakpien S, et  
583 al. Female tiger *panthera tigris* home range size and prey abundance: Important metrics  
584 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](https://www.cambridge.org/core/product/identifier/S0030605312001408/type/journal_article)
- 586 57. Watson J. Ferruginous hawk (*buteo regalis*) home range and resource use on northern  
587 grasslands in canada. 2020 [cited 2022 Nov 8]; Available from: <http://rgdoi.net/10.13140/RG.2.2.32404.32648>
- 589 58. Levin SA. The problem of pattern and scale in ecology: The robert h. MacArthur  
590 award lecture. Ecology [Internet]. 1992 [cited 2024 Jan 31];73:1943–67. Available from:  
591 <https://esajournals.onlinelibrary.wiley.com/doi/10.2307/1941447>

- 592 59. Steixner-Kumar S, Gläscher J. Strategies for navigating a dynamic world. *Science*  
593 [Internet]. 2020 [cited 2022 Mar 9];369:1056–7. Available from: <https://www.science.org/doi/10.1126/science.abd7258>
- 595 60. Mueller T, O'Hara RB, Converse SJ, Urbanek RP, Fagan WF. Social learning of mi-  
596 gratory performance. *Science* [Internet]. 2013 [cited 2022 Nov 24];341:999–1002. Available  
597 from: <https://www.science.org/doi/10.1126/science.1237139>
- 598 61. Abrahms B, Hazen EL, Aikens EO, Savoca MS, Goldbogen JA, Bograd SJ, et al. Memory  
599 and resource tracking drive blue whale migrations. *Proc Natl Acad Sci USA* [Internet]. 2019  
600 [cited 2022 Mar 3];116:5582–7. Available from: <http://www.pnas.org/lookup/doi/10.1073/pnas.1819031116>
- 602 62. Falcón-Cortés A, Boyer D, Merrill E, Frair JL, Morales JM. Hierarchical, memory-based  
603 movement models for translocated elk (*cervus canadensis*). *Front Ecol Evol* [Internet]. 2021  
604 [cited 2022 Feb 4];9:702925. Available from: <https://www.frontiersin.org/articles/10.3389/fevo.2021.702925/full>
- 606 63. Fagan WF, Lewis MA, Auger-Méthé M, Avgar T, Benhamou S, Breed G, et al. Spatial  
607 memory and animal movement. Clobert J, editor. *Ecol Lett* [Internet]. 2013 [cited 2022  
608 Mar 9];16:1316–29. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/ele.12165>
- 609 64. Logares R, Nuñez M. Black swans in ecology and evolution: The importance of improba-  
610 ble but highly influential events. *Ideas in Ecology and Evolution* [Internet]. 2012 [cited 2020  
611 Feb 12]; Available from: <https://ojs.library.queensu.ca/index.php/IEE/article/view/4311>
- 612 65. Anderson SC, Branch TA, Cooper AB, Dulvy NK. Black-swan events in animal

613 populations. Proceedings of the National Academy of Sciences [Internet]. 2017 [cited  
614 2020 Jan 24];114:3252–7. Available from: <http://www.pnas.org/lookup/doi/10.1073/pnas.1611525114>

616 66. Riotte-Lambert L, Matthiopoulos J. Environmental predictability as a cause and  
617 consequence of animal movement. Trends in Ecology & Evolution [Internet]. 2020 [cited  
618 2020 Nov 11];35:163–74. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S0169534719302885>

620 67. Levins RA. Evolution in changing environments: Some theoretical explorations. 3.  
621 printing. Princeton, NJ: Princeton Univ. Press; 1974.

622 68. Van Baalen M, Křivan V, Van Rijn PCJ, Sabelis MW. Alternative food, switching  
623 predators, and the persistence of predator-prey systems. The American Naturalist [Internet].  
624 2001 [cited 2024 May 20];157:512–24. Available from: <https://www.journals.uchicago.edu/doi/10.1086/319933>

626 69. Fleming CH, Calabrese JM. Ctmm: Continuous-time movement modeling [Internet].  
627 2021. Available from: <https://github.com/ctmm-initiative/ctmm>, <https://groups.google.com/g/ctmm-user>

629 70. R Core Team. R: A language and environment for statistical computing [Internet].  
630 Vienna, Austria: R Foundation for Statistical Computing; 2023. Available from: <https://www.R-project.org/>

632 71. Gurarie E, Fleming CH, Fagan WF, Laidre KL, Hernández-Pliego J, Ovaskainen O.  
633 Correlated velocity models as a fundamental unit of animal movement: Synthesis and

634 applications. *Mov Ecol* [Internet]. 2017 [cited 2023 Sep 6];5:13. Available from: <http://movementecologyjournal.biomedcentral.com/articles/10.1186/s40462-017-0103-3>

636 72. Fleming CH, Calabrese JM, Mueller T, Olson KA, Leimgruber P, Fagan WF. From  
637 fine-scale foraging to home ranges: A semivariance approach to identifying movement modes  
638 across spatiotemporal scales. *The American Naturalist* [Internet]. 2014 [cited 2022 Jul  
639 26];183:E154–67. Available from: <https://www.journals.uchicago.edu/doi/10.1086/675504>

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

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

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

650 76. Noonan MJ, Tucker MA, Fleming CH, Akre TS, Alberts SC, Ali AH, et al. A comprehen-  
651 sive analysis of autocorrelation and bias in home range estimation. *Ecological Monographs*  
652 [Internet]. 2019 [cited 2020 Oct 23];89:e01344. Available from: <https://onlinelibrary.wiley.com/doi/abs/10.1002/ecm.1344>

654 77. Alston JM, Fleming CH, Kays R, Streicher JP, Downs CT, Ramesh T, et al. Mitigat-

655 ing pseudoreplication and bias in resource selection functions with autocorrelation-informed  
656 weighting. *Methods Ecol Evol* [Internet]. 2022 [cited 2022 Dec 12];2041–210X.14025. Available  
657 from: <https://onlinelibrary.wiley.com/doi/10.1111/2041-210X.14025>

658 78. Silva I, Fleming CH, Noonan MJ, Alston J, Folta C, Fagan WF, et al. Autocorrelation-informed  
659 home range estimation: A review and practical guide. *Methods Ecol Evol*  
660 [Internet]. 2022 [cited 2022 Jul 26];13:534–44. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/2041-210X.13786>

662 79. Wood SN, Pya N, Säfken B. Smoothing parameter and model selection for general  
663 smooth models. *Journal of the American Statistical Association* [Internet]. 2016 [cited  
664 2020 Apr 3];111:1548–63. Available from: <https://www.tandfonline.com/doi/full/10.1080/01621459.2016.1180986>

666 80. Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. Toward a metabolic theory  
667 of ecology. *Ecology* [Internet]. 2004 [cited 2022 Mar 3];85:1771–89. Available from: <http://doi.wiley.com/10.1890/03-9000>

669 81. Johnson DH. The comparison of usage and availability measurements for evaluating  
670 resource preference. *Ecology* [Internet]. 1980 [cited 2024 May 17];61:65–71. Available from:  
671 <https://esajournals.onlinelibrary.wiley.com/doi/10.2307/1937156>

672 82. Rickbeil GJM, Merkle JA, Anderson G, Atwood MP, Beckmann JP, Cole EK, et  
673 al. Plasticity in elk migration timing is a response to changing environmental conditions.  
674 *Glob Change Biol* [Internet]. 2019 [cited 2022 Jan 20];25:2368–81. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/gcb.14629>

- 676 83. Ranc N, Cagnacci F, Moorcroft PR. Memory drives the formation of animal home ranges:  
677 Evidence from a reintroduction. Coulson T, editor. *Ecology Letters* [Internet]. 2022 [cited  
678 2022 Nov 16];25:716–28. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/ele.13869>
- 680 84. Nespolo RF, Mejias C, Bozinovic F. Why bears hibernate? Redefining the scaling  
681 energetics of hibernation. *Proc R Soc B* [Internet]. 2022 [cited 2022 Nov 21];289:20220456.  
682 Available from: <https://royalsocietypublishing.org/doi/10.1098/rspb.2022.0456>
- 683 85. Goldberg AR, Conway CJ. Hibernation behavior of a federally threatened ground  
684 squirrel: Climate change and habitat selection implications. Hayes L, editor. *Journal*  
685 of Mammalogy [Internet]. 2021 [cited 2022 Nov 21];102:574–87. Available from: <https://academic.oup.com/jmammal/article/102/2/574/6224539>
- 687 86. Reher S, Ehlers J, Rabarison H, Dausmann KH. Short and hyperthermic torpor responses  
688 in the malagasy bat *macronycteris commersoni* reveal a broader hypometabolic scope in  
689 heterotherms. *J Comp Physiol B* [Internet]. 2018 [cited 2022 Oct 3];188:1015–27. Available  
690 from: <http://link.springer.com/10.1007/s00360-018-1171-4>
- 691 87. Mohr SM, Bagriantsev SN, Gracheva EO. Cellular, molecular, and physiological adap-  
692 tations of hibernation: The solution to environmental challenges. *Annu Rev Cell Dev Biol*  
693 [Internet]. 2020 [cited 2022 Oct 3];36:315–38. Available from: <https://www.annualreviews.org/doi/10.1146/annurev-cellbio-012820-095945>
- 695 88. Merkle JA, Sawyer H, Monteith KL, Dwinnell SPH, Fralick GL, Kauffman MJ. Spatial  
696 memory shapes migration and its benefits: Evidence from a large herbivore. Gaillard J,  
697 editor. *Ecol Lett* [Internet]. 2019 [cited 2022 Sep 5];22:1797–805. Available from: <https://>

698 //onlinelibrary.wiley.com/doi/10.1111/ele.13362

699 89. Fretwell SD, Lucas HL. On territorial behavior and other factors influencing habitat  
700 distribution in birds: I. Theoretical development. *Acta Biotheor* [Internet]. 1969 [cited 2024  
701 Apr 8];19:16–36. Available from: <http://link.springer.com/10.1007/BF01601953>

702 90. Ciuti S, Northrup JM, Muhly TB, Simi S, Musiani M, Pitt JA, et al. Effects of humans  
703 on behaviour of wildlife exceed those of natural predators in a landscape of fear. Moreira  
704 N, editor. *PLoS ONE* [Internet]. 2012 [cited 2022 Aug 11];7:e50611. Available from: <https://dx.plos.org/10.1371/journal.pone.0050611>

706 91. Burson A, Stomp M, Greenwell E, Grosse J, Huisman J. Competition for nutrients  
707 and light: Testing advances in resource competition with a natural phytoplankton com-  
708 munity. *Ecology* [Internet]. 2018 [cited 2022 Sep 2];99:1108–18. Available from: <https://onlinelibrary.wiley.com/doi/10.1002/ecy.2187>

710 92. Phillips LB, Hansen AJ, Flather CH. Evaluating the species energy relationship with the  
711 newest measures of ecosystem energy: NDVI versus MODIS primary production. *Remote  
712 Sensing of Environment* [Internet]. 2008 [cited 2024 Feb 14];112:4381–92. Available from:  
713 <https://linkinghub.elsevier.com/retrieve/pii/S0034425708002460>

714 93. Seigle-Ferrand J, Atmeh K, Gaillard J-M, Ronget V, Morellet N, Garel M, et al. A  
715 systematic review of within-population variation in the size of home range across ungulates:  
716 What do we know after 50 years of telemetry studies? *Front Ecol Evol* [Internet]. 2021 [cited  
717 2022 Aug 16];8:555429. Available from: <https://www.frontiersin.org/articles/10.3389/fevo.2020.555429/full>

- 719 94. Merkle JA, Monteith KL, Aikens EO, Hayes MM, Hersey KR, Middleton AD, et al.  
720 Large herbivores surf waves of green-up during spring. Proc R Soc B [Internet]. 2016 [cited  
721 2024 Feb 14];283:20160456. Available from: <https://royalsocietypublishing.org/doi/10.1098/rspb.2016.0456>
- 723 95. Gautam H, Arulmalar E, Kulkarni MR, Vidya TNC. NDVI is not reliable as a surrogate  
724 of forage abundance for a large herbivore in tropical forest habitat. Biotropica [Internet].  
725 2019 [cited 2024 Feb 14];51:443–56. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/btp.12651>
- 727 96. Huang S, Tang L, Hupy JP, Wang Y, Shao G. A commentary review on the use of  
728 normalized difference vegetation index (NDVI) in the era of popular remote sensing. J For  
729 Res [Internet]. 2021 [cited 2024 Feb 14];32:1–6. Available from: <https://link.springer.com/10.1007/s11676-020-01155-1>
- 731 97. Fan X, Liu Y. A global study of NDVI difference among moderate-resolution satel-  
732 lite sensors. ISPRS Journal of Photogrammetry and Remote Sensing [Internet]. 2016  
733 [cited 2024 Feb 14];121:177–91. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S0924271616303975>
- 735 98. Prox L, Farine D. A framework for conceptualizing dimensions of social organization  
736 in mammals. Ecol Evol [Internet]. 2020 [cited 2022 Aug 23];10:791–807. Available from:  
737 <https://onlinelibrary.wiley.com/doi/10.1002/ece3.5936>
- 738 99. Grant JWA. Whether or not to defend? The influence of resource distribution. Marine  
739 Behaviour and Physiology [Internet]. 1993 [cited 2022 Feb 3];23:137–53. Available from:  
740 <http://www.tandfonline.com/doi/abs/10.1080/10236249309378862>

- 741 100. Martinez-Garcia R, Fleming CH, Seppelt R, Fagan WF, Calabrese JM. How range  
742 residency and long-range perception change encounter rates. *Journal of Theoretical Biology*  
743 [Internet]. 2020 [cited 2022 Mar 11];498:110267. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S0022519320301223>
- 745 101. Tian F, Fensholt R, Verbesselt J, Grogan K, Horion S, Wang Y. Evaluating tem-  
746 poral consistency of long-term global NDVI datasets for trend analysis. *Remote Sensing*  
747 of Environment [Internet]. 2015 [cited 2024 Feb 14];163:326–40. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S0034425715001285>
- 749 102. Wood SN. Generalized additive models: An introduction with r. Second edition. Boca  
750 Raton: CRC Press/Taylor & Francis Group; 2017.
- 751 103. Nathan R, Monk CT, Arlinghaus R, Adam T, Alós J, Assaf M, et al. Big-data ap-  
752 proaches lead to an increased understanding of the ecology of animal movement. *Science*  
753 [Internet]. 2022 [cited 2022 Mar 9];375:eabg1780. Available from: <https://www.science.org/doi/10.1126/science.abg1780>
- 755 104. Wood SN, Li Z, Shaddick G, Augustin NH. Generalized additive models for gigadata:  
756 Modeling the u.k. Black smoke network daily data. *Journal of the American Statistical  
757 Association* [Internet]. 2017 [cited 2022 Mar 11];112:1199–210. Available from: <https://www.tandfonline.com/doi/full/10.1080/01621459.2016.1195744>
- 759 105. Intergovernmental Panel On Climate Change. *Climate change 2021 – the physical  
760 science basis: Working group i contribution to the sixth assessment report of the intergov-  
761 ernmental panel on climate change* [Internet]. 1st ed. Cambridge University Press; 2023  
762 [cited 2023 Jun 30]. Available from: <https://www.cambridge.org/core/product/identifier/>

<sub>763</sub> 9781009157896/type/book

<sub>764</sub> 106. Grant PR, Grant BR, Huey RB, Johnson MTJ, Knoll AH, Schmitt J. Evolution caused  
<sub>765</sub> by extreme events. *Phil Trans R Soc B* [Internet]. 2017 [cited 2022 Nov 18];372:20160146.  
<sub>766</sub> Available from: <https://royalsocietypublishing.org/doi/10.1098/rstb.2016.0146>

<sub>767</sub> 107. Rypkema D, Tuljapurkar S. Modeling extreme climatic events using the generalized ex-  
<sub>768</sub> treme value (GEV) distribution. *Handbook of statistics* [Internet]. Elsevier; 2021 [cited  
<sub>769</sub> 2023 Oct 18]. p. 39–71. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S0169716120300511>

<sub>771</sub> 108. Yao Q, Fan J, Meng J, Lucarini V, Jensen HJ, Christensen K, et al. Emergence  
<sub>772</sub> of universal scaling in weather extreme events. 2022 [cited 2022 Nov 20]; Available from:  
<sub>773</sub> <https://arxiv.org/abs/2209.02292>