

How resource abundance and stochasticity affect organisms' range sizes

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## **1 Abstract**

2 The amount of space organisms use is thought to be tightly linked to the availability of  
3 resources within their habitats, such that organisms living in productive habitats generally  
4 require less space than those in resource-poor habitats. This hypothesis has widespread 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.

<sup>17</sup> **Introduction**

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

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

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

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

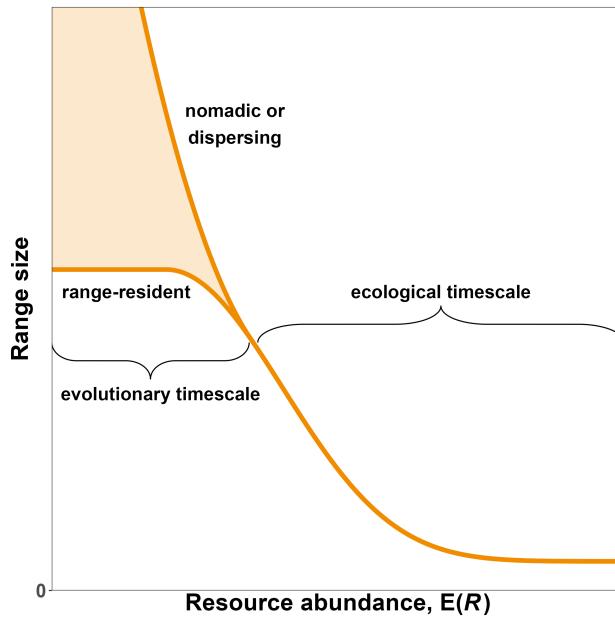
80 Resources are often unpredictable (and difficult to quantify), since they depend on various  
81 factors which cannot be accounted for easily, including climate (Lindstedt and Boyce 1985;  
82 Schmidt et al. 2020; Morellet et al. 2013), weather (Fjelldal, Wright, and Stawski 2021;  
83 Morellet et 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.

<sup>92</sup> **Effects of resource abundance,  $E(R)$**

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

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

<sup>119</sup> facilitated by morphological features such as hinged joints and elongated limbs (Jetz et al.  
<sup>120</sup> 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  $E(R)$ .

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

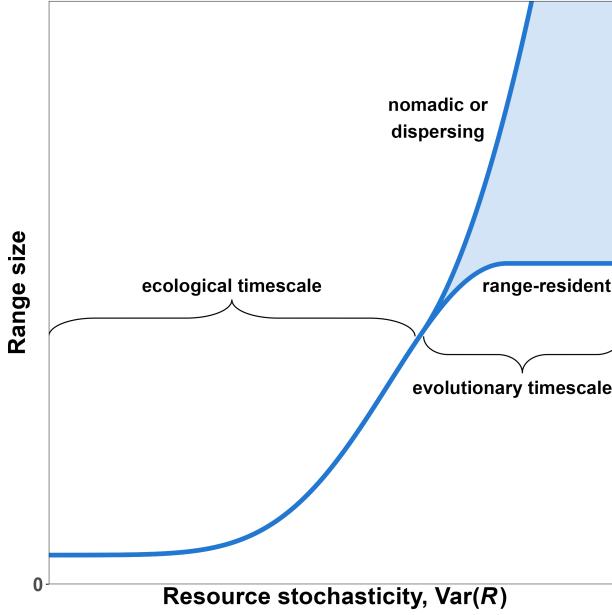
132 **Effects of resource stochasticity,  $\text{Var}(R)$**

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.

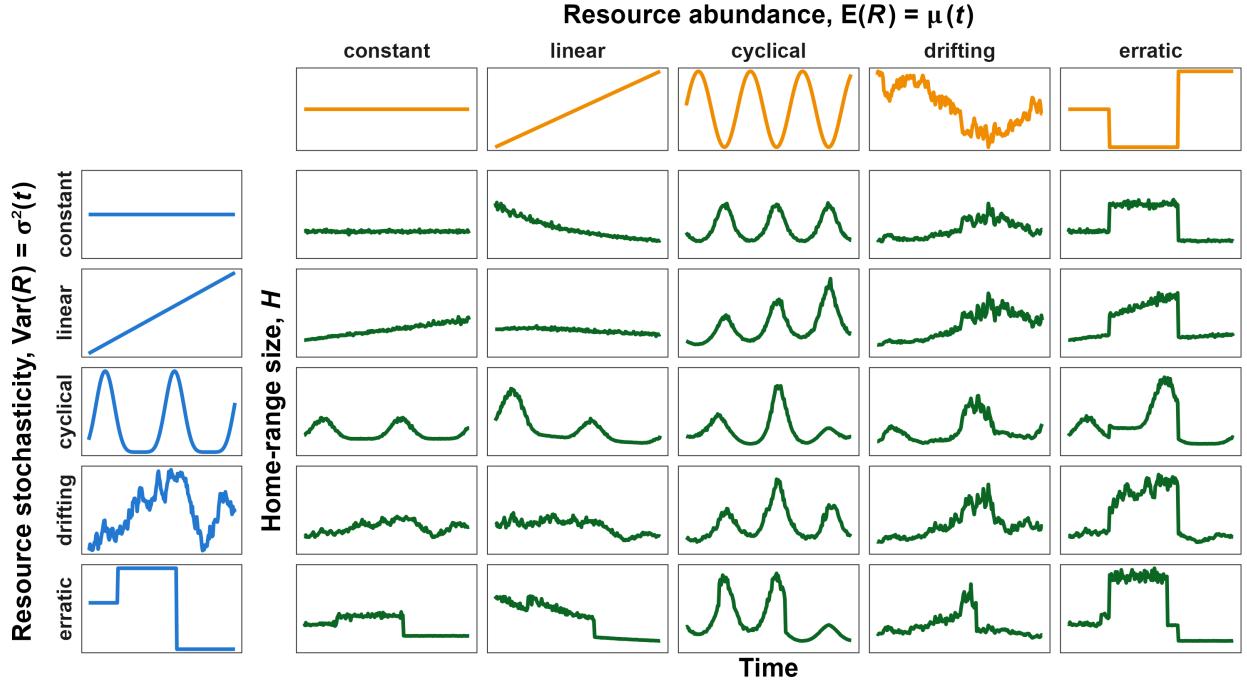
217 We designed the simulations to estimate the effects of  $E(R)$  and  $\text{Var}(R)$  in simplistic  
218 environments where organisms could only respond by searching for longer periods of time.

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. C3 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

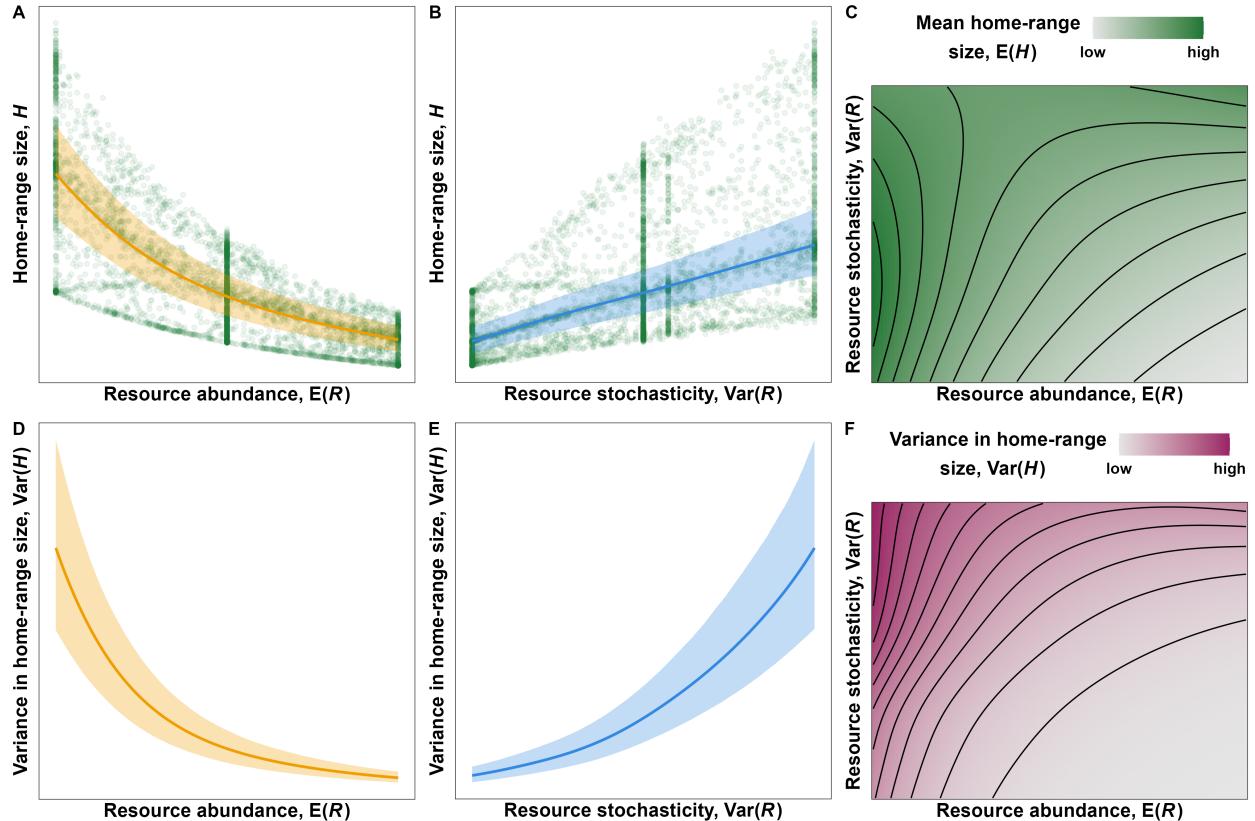
259 the effects can be particularly difficult when both parameters change in a correlated manner  
260 (e.g., linear  $E(R)$  and  $\text{Var}(R)$ ). When both  $E(R)$  and  $\text{Var}(R)$  increase linearly,  $H$  initially  
261 increases since the effect of  $\text{Var}(R)$  is stronger, but then 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).

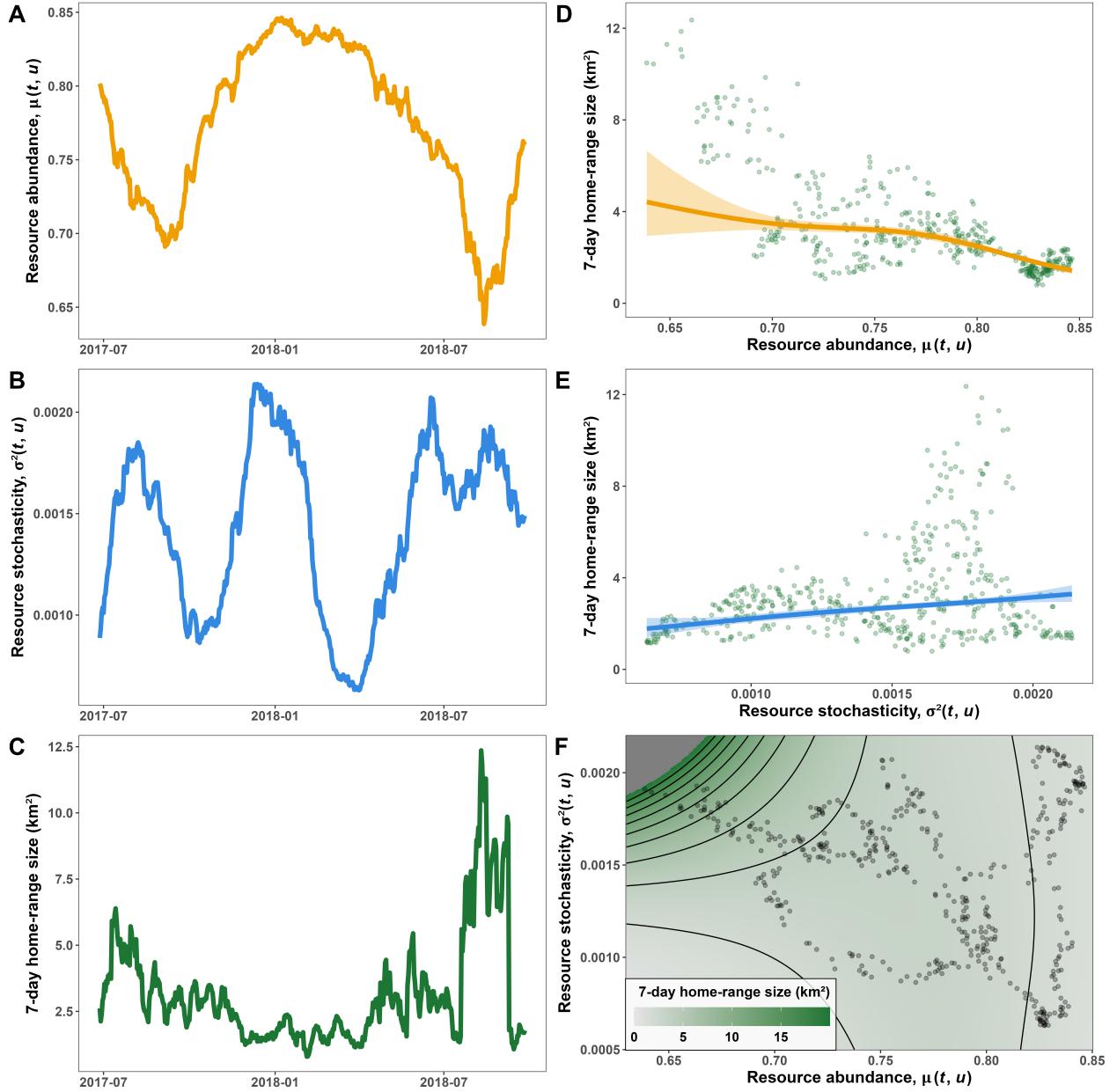
295 Fig. 5 illustrates how a tapir in the Brazilian Cerrado adapts its 7-day home-range size to  
296 spatiotemporal changes in  $\mu(t, u)$  and  $\sigma^2(t, u)$  (telemetry data from the individual labelled  
297 as “Anna” in the dataset from Medici et al. 2022). Panels A and B show the changes in  
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 km<sup>2</sup>; 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 to  
330 resource dynamics can be complex. The simulated and empirical results suggest qualitatively  
331 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  
333 a strong effect when  $E(R)$  is high, while the opposite is true for the empirical data. This  
334 is due to two reasons. Firstly, the shape and symmetry of bounded distributions such as  
335 Gamma ( $R > 0$ ) and Beta ( $0 < R < 1$ ) distributions depend on both  $E(R)$  and  $\text{Var}(R)$  (figs.  
336 A3, 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 Maloiy 1982), movement speed (Taylor,  
355 Heglund, and Maloiy 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 Examples of ecosystem-level biases are the effects of competition, predation, habitat  
392 connectivity, and movement costs, all of which can depend on habitat quality, and, con-  
393 sequently, be correlated nonlinearly to  $R$  and NDVI (Jetz et al. 2004; Prox and Farine  
394 2020). Resource-rich patches can attract larger amounts of competitors (Kacelnik, Krebs,  
395 and Bernstein 1992) and predators (Duncan et al. 2015), which may, in turn, increase pres-  
396 sures from competition and predation (Charnov 1976; J. S. Brown, Laundre, and Gurung  
397 1999). However, such pressures may result in both an expansion of the range (Jetz et al.  
398 2004; Prox and Farine 2020) or a contraction, since larger ranges can be harder to defend  
399 and result in higher movement costs (J. W. A. Grant 1993; Jetz et al. 2004) and encounter  
400 rates (Martinez-Garcia et al. 2020).

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

## 408 Conclusion

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

414 Recent advances in computational power have greatly increased analysts' ability to fit  
415 computationally demanding models (Nathan et al. 2022; Wood et al. 2017) that allow

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

<sup>422</sup> **Conflict of interest**

<sup>423</sup> The authors declare there are no conflicts of interest.

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