

# What's in a resource gradient? Comparing alternative cues for foraging in dynamic environments via movement, perception, and memory

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WHAT'S IN A RESOURCE GRADIENT ?

COMPARING ALTERNATIVE CUES FOR FORAGING IN DYNAMIC ENVIRONMENTS  
VIA MOVEMENT, PERCEPTION, AND MEMORY

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18 ABSTRACT

19 Consumers must track and acquire resources in complex landscapes. Much discussion has  
20 focused on the concept of a ‘resource gradient’ and the mechanisms by which consumers can  
21 take advantage of such gradients as they navigate their landscapes in search of resources.  
22 However, the concept of tracking resource gradients means different things in different contexts.  
23 Here we take a synthetic approach and consider six different definitions of what it means to  
24 search for resources based on density or gradients in density. These include scenarios where  
25 consumers change their movement behavior based on the density of conspecifics, on the density  
26 of resources, and on spatial or temporal gradients in resources. We also consider scenarios  
27 involving non-local perception and a form of memory. Using a continuous space, continuous  
28 time model that allows consumers to switch between resource-tracking and random motion, we  
29 investigate the relative performance of these six different strategies. Consumers’ success in  
30 matching the spatiotemporal distributions of their resources differs starkly across the six  
31 scenarios. Movement strategies based on perception and response to temporal (rather than  
32 spatial) resource gradients afforded consumers with the best opportunities to match resource  
33 distributions. All scenarios would allow for optimization of resource matching in terms of the  
34 underlying parameters, providing opportunities for evolutionary adaptation, and links back to  
35 classical studies of foraging ecology.

36

37 INTRODUCTION

38         Successful acquisition of resources is essential to an individual’s survival and  
39 reproduction. The acquisition problem is especially challenging in seasonal or otherwise  
40 dynamic landscapes where the spatial location of resources changes over time. This absence of  
41 consistently available resources leaves consumers with several options. Consumers may track

42 the shifting positions of resources that themselves move across the landscape, they may move to  
43 other regions to take advantage of different resources, or they may stay local but switch to  
44 alternative resources. Each of these foraging strategies requires that consumers monitor resource  
45 availability and respond through movement or changes in feeding style. However, many routes  
46 to resource monitoring and movement decision-making exist, and different strategies are unlikely  
47 to exhibit the same level of profitability with regard to resource acquisition (Grünbaum 1998).  
48 Historically, researchers working on foraging-related movement have sought to understand the  
49 contributions of three elements: search strategies, behavioral changes, and cues for movement.  
50 Here, we bring together these three elements in a synthetic approach that investigates how  
51 consumers' responses to alternative 'resource gradients' translate into foraging success.

52         As consumers seek out resources, they can employ a wide variety of search strategies.  
53 Some of these strategies operate on large scales and are long-term in nature. For example, some  
54 birds and ungulates 'surf the green wave' as they time their migratory journeys to match seasonal  
55 changes in the availability of palatable, nutrient-rich resources as functions of latitude or  
56 elevation (Aikens et al. 2020). In other taxa, such as some Brazilian marsupials, perceptual  
57 range plays a key role in determining whether the animals move randomly (when no forest was  
58 nearby) or in a directed fashion (when they could perceive a nearby forest patch) (Prevedello et  
59 al. 2011). Similarly, Holdo et al. (2009) found that long-distance perception that allowed  
60 tracking of conditions over large spatial scales was crucial to the success of wildebeests'  
61 migratory journeys in the Serengeti and attention solely to small-scale gradients was insufficient  
62 for migratory success. In contrast, blue whales appear to rely not on perception per se, but  
63 rather on spatial memory as they migrate. The whales time their patterns of space use to exploit

64 those regions in which resources have been both on average abundant and reliably available over  
65 many years (Abrahms et al. 2019, Fagan 2019).

66 Evidence suggests that such search strategies do not exist in isolation, but rather are used  
67 by consumers in different combinations, often as a function of context. With regard to switching  
68 between search strategies, a key tension is between searching for new resources and not  
69 wandering too far. This is particularly important when resources are spatiotemporally  
70 heterogeneous. Mathematically, this tension can appear as a balance between random search  
71 (diffusion) and range residency (movement with a central tendency) as animals switch between  
72 movement modes as a function of their spatial context. A growing list of empirical examples  
73 demonstrates that such context-dependent behavioral switching between movement modes is  
74 quite widespread. A few examples include mosquitoes (Rjo and DeGennaro 2017), tuna  
75 (Newlands et al. 2004), opossums (Prevedello et al. 2011), elk (Morales et al. 2004), and  
76 woodpeckers (Vergara et al. 2018). Moreover, robust statistical tools are increasingly available  
77 for deconstructing empirical movement paths into alternative movement modes and identifying  
78 behavioral change points (Morales et al. 2004, Gurarie et al. 2009, 2016). Key open questions  
79 center on the factors that precipitate such changes in behavior and how different forms of  
80 context-dependent switching influence resource acquisition.

81 To some degree, modeling studies have also explored the consequences of combining  
82 movement modes in various mixtures. Frequently, diffusion (random search) and advection  
83 (gradient following) are explored together, often with the goal of identifying optimally blended  
84 movement strategies that yield evolutionarily stable strategies (Cantrell et al. 2008, 2018, 2020;  
85 Lam and Lou 2014). Other modeling studies have directly considered switching between  
86 alternative movement modes; that is, they explored situations where, rather than simultaneously

87 blending two movement modes, individuals could be considered to be in either one movement  
88 mode or another. Skalski and Gilliam (2003) explored how switching between slow and fast  
89 movement states (which occurred independent of spatial context) influenced a population's  
90 spatial distribution. More recently, Tyson et al. (2011) considered spatially independent  
91 behavioral switching terms for a model where foragers had both fast-moving diffusive and slow-  
92 moving advective-diffusive states. They found that single-movement-mode models (in which the  
93 forager population was homogeneously diffusive or advective-diffusive) provided a worse fit to  
94 data for both caribou and honeybees than did the model with behavioral switching. Different  
95 types of intermittent movement (Gleiss et al. 2011), especially so-called burst-and-coast  
96 movement by fish (Kramer and McLaughlin 2001, McLaughlin and Grant 2001), provide yet  
97 more examples in which animals sequentially switch between movement types. Burst movement  
98 is thought to provide rapid propulsion that alternates with coast movement during which fish can  
99 better perceive their surroundings. Fagan et al. (2020) analyzed a model in which switching  
100 between movement modes depended on spatial context. They found that behavioral switching  
101 was most beneficial when an organism's gradient-following abilities were weak compared to its  
102 overall capacity for movement. Moreover, they found that an organism's perceptual range was a  
103 key determinant of whether behavioral switching was advantageous or disadvantageous in the  
104 search for resources.

105         Just as different movement strategies, and opportunities for switching between strategies,  
106 present consumers with a range of options for mobility, so too do the proximal cues on which  
107 resource-related movement decisions are based. For example, Dusenberry (1998) demonstrated  
108 that free-swimming bacteria can be differentially advantaged by using temporal gradients versus  
109 spatial gradients in their quest for resources. In that system, movements based on following

110 temporal gradients were especially valuable in providing superior access to resources when those  
111 resources were at low densities. In another example, numerous species of tropical frugivorous  
112 birds appear to track temporal changes in fruit abundance, shifting their spatial activity in  
113 response to increases and decreases in fruit abundance (Loiselle and Blake 1991). In other cases,  
114 following spatial rather than temporal gradients appears essential to success, and small scale  
115 spatial gradients are particularly useful for consumers that rely on chemosensation. For example,  
116 catfish follow centimeter-scale spatial (rather than temporal) gradients in nutrient concentration  
117 as they seek out resources (Johnson and Teeter 1980). Similarly, rats effectively ‘smell in  
118 stereo’ as they respond to highly localized bilateral differences in the concentration of odorants  
119 (Rajan et al. 2006), whereas moles combine serial scent detection (i.e., repeated ‘sniffing’) with  
120 bilateral olfaction to identify the gradients that guide their search for resources (Catania 2013).

121 Here we seek to synthesize these three factors (i.e., alternative search strategies,  
122 switching between movement modes, and diverse cues for movement) into a single modeling  
123 framework to explore in detail how these features influence the abilities of consumers to track  
124 and match the spatiotemporal distribution of resources in dynamic landscapes. Intriguingly, we  
125 find that different search-movement strategies perform best under different resource situations,  
126 suggesting conditions under which alternative resource dynamics might select for the evolution  
127 of alternative foraging strategies.

## 128 METHODS

129 A dynamic resource: We will assume a one-dimensional binary resource landscape of habitat  
130 patches and non-habitat that is temporally dynamic. Fagan et al. (2017) explored how alternative  
131 resource functions influence the ability of consumers to match the distribution of their resources.

132 Here, we consider one of the resource functions studied in that paper, the Pulsed Gaussian  
133 resource:

$$134 \quad m(x, t) = \frac{1}{\sqrt{2\pi}\sigma} \exp\left(-\frac{(x-\mu)^2}{2\sigma^2}\right) \sin^2(\omega t/2) \quad (1)$$

135 where  $\mu$  and  $\sigma$  are, respectively, the mean and standard deviation of the resource pulse and  $\omega$  is  
136 the temporal frequency of the pulse. Equation (1) corresponds to a resource patch with smoothly  
137 varying edges that does not change position spatially but does increase and decrease in  
138 abundance over time.

139 We consider situations in which there either is a single resource patch that pulses in time  
140 or two identical pulsing resource patches that are shifted by half a period relative to one another.  
141 The latter scenario corresponds to a strongly seasonal landscape where there exists opportunity  
142 for migration to emerge between the two resource patches that are oscillating out-of-phase.

143 Consumers Switch between Random Search and Range-residency: Living on this dynamic  
144 resource landscape is a population of consumers. We consider a population in which the  
145 consumers can switch between two distinct modes of dispersal. Tyson et al. (2011) and Fagan et  
146 al. (2019) explored scenarios in which consumers switch between a random search mode and a  
147 mode in which there exists movement in response to a resource gradient. Here, motivated by  
148 recent developments in the statistical analysis of animal tracking data (Fleming et al. 2014,  
149 Noonan et al. 2019), we do something a bit different. Specifically, we consider the spatial  
150 dynamics of consumers that may have home ranges, but which can switch between a random  
151 search mode and a range-resident mode. Note that this pair of movement modes is different than  
152 the pair of modes involved in chemotaxis (Keller and Segel 1971) and area-restricted search  
153 models (Kareiva and Odell 1987). In those cases, organisms can switch between random turning  
154 (employed within a resource patch) and ballistic motion (employed between resource patches).

155 Here, motivated by recent studies on some vertebrate species (Prevedello et al. 2011, Tyson et al.  
 156 2011), our foragers use random motion between resource patches and their more sophisticated  
 157 (and more spatially intensive) movement mode (here, home ranging) in the vicinity of resource  
 158 patches.

159 To build our model of movement, we assume that the density of the population engaged  
 160 in diffusive (random search) behavior at position  $x$  and time  $t$  is denoted  $u(x,t)$ , and the density  
 161 engaged in range-resident behavior is denoted  $v(x,t)$ . We write

$$\begin{aligned}
 \frac{\partial u(x,t)}{\partial t} &= \overbrace{D \frac{\partial^2}{\partial x^2} u}^{\text{random search}} - \overbrace{\alpha(x,t)u}^{\text{switching from random search}} + \overbrace{\beta(x,t)v}^{\text{switching to random search}} \\
 \frac{\partial v(x,t)}{\partial t} &= \left[ \overbrace{\varepsilon \frac{\partial^2}{\partial x^2} v}^{\text{low level random movement}} + \overbrace{\theta \frac{d}{dx} (x - \mu)v}^{\text{home ranging central tendency}} \right] + \overbrace{\alpha(x,t)u}^{\text{switching to range residency}} - \overbrace{\beta(x,t)v}^{\text{switching from range residency}}
 \end{aligned} \tag{2}$$

163 where the parameter  $D$  is the rate of diffusion undertaken by the portion of the population that is  
 164 in the random search mode. The functions  $\alpha(x,t)$  and  $\beta(x,t)$ , defined below, are generic  
 165 functional forms for the rates of switching between the random-search and range-resident  
 166 movement modes. The term

$$\varepsilon \frac{\partial^2}{\partial x^2} v + \theta \frac{d}{dx} (x - \mu)v \tag{3}$$

168 represents the overall movement of the portion of the population engaged in range resident  
 169 behavior. In (3),  $\varepsilon \ll 1$  represents a small amount of background random movement (this is  
 170 necessary for certain theorems about partial differential equations to hold true), and  $\theta$  quantifies  
 171 the rate of mean reverting (home ranging) movement. The term  $\mu$  (from Eq. 1) represents the  
 172 consumers' 'attractive target.' This corresponds to the center of the resource patch in scenarios

173 where there is only a single, fluctuating area with resources. This location  $\mu$  could also be  
174 thought of as the location of a den or nest site. In more complicated scenarios,  $\mu$  could be  
175 generalized to a function,  $x[\cdot]$ , that allows for more than one attractive target, and these could  
176 correspond to the physical centers of multiple or temporally oscillating resource patches. In other  
177 scenarios, where consumers are able to distinguish resource habitat from non-habitat, but where  
178 perception is limited and the physical center of a resource patch may not be detectable, the  
179 attractive target could correspond to a location with favorable conditions inside the patch at the  
180 limit of detection.

181 Six Scenarios for Switching Between Movement Modes: To explore the interplay between  
182 movement modes, search strategies, and cues for movement, we focus on the switching functions  
183  $\alpha(x, t)$  and  $\beta(x, t)$  and the impacts that these terms have on the ability of the consumers to track  
184 their resources. To explore the importance of the context of behavioral switching, we simplify  
185 other aspects of the model, and depart from previous treatments in Fagan et al. (2017, 2020) and  
186 Gurarie et al. (2021). We consider six different scenarios, of increasing complexity, in which  
187 different considerations govern the consumers' switching between random movement and home-  
188 ranging behavior. All six of these scenarios, which range from simple density dependence  
189 through more complicated situations involving perception or spatial memory, have either been  
190 utilized previously in theoretical studies of animal movement or discussed verbally in papers on  
191 animal movement and decision-making behavior (e.g., Noonan et al. 2019, Abrahms et al. 2019,  
192 Aikens et al. 2020).

193 Scenario 1: Switching Depends on Consumer Density. In this scenario, we assume that  
194 consumers change between the random search and range resident behavior only as a function of  
195 their own density. That is, these consumers are not able to detect or react to changes in resource

196 availability (in space, or in time) but they can tell when they are crowded, and switch behaviors  
 197 as functions of the density of their conspecifics. We write

$$198 \quad \alpha_{S1}(x, t) = \begin{cases} s & \text{if } u + v > w_0 \\ 0 & \text{if } u + v \leq w_0 \end{cases}, \quad (4)$$

199 which means that consumers will switch from random search mode to range resident mode at  
 200 rate  $s$  if the local total consumer density ( $u + v$ ) exceeds a threshold value,  $w_0$ , and will  
 201 otherwise remain in random search mode. Similarly,

$$202 \quad \beta_{S1}(x, t) = \begin{cases} 0 & \text{if } u + v > w_0 \\ s & \text{if } u + v \leq w_0 \end{cases}, \quad (5)$$

203 such that consumers will switch from range residency to random search mode at rate  $s$  if the  
 204 local total consumer density ( $u + v$ ) remains below a threshold value,  $w_0$ , and will otherwise  
 205 remain in range resident mode. For simplicity, we will consider the switching rates in Equations  
 206 (4-5) to be the same, but these could certainly differ as a function of the consumers' current  
 207 behavioral mode, as could the threshold density for switching between movement modes.

208         These assumptions correspond roughly to assumptions of the ‘local enhancement’  
 209 framework for seabirds foraging from colonies (Buckley 1997). Likewise, there are conceptual  
 210 connections to results described in Cvikel et al. (2015) and Egert-Berg et al. (2018), wherein bats  
 211 cue in on the location of their own kind in determining where to forage. However, the model  
 212 does not lead to aggregation on conspecifics per se (unless  $\theta = 0$ ). Instead, the model would be  
 213 better interpreted as representing aspects of social learning with discovery. To see this, consider  
 214 the subpopulation with density  $u$  as ‘uninformed about resources’ and the subpopulation with  
 215 density  $v$  as ‘informed.’ Then, note that  $v(x, 0) = 0$  and  $u(x, 0) = u_0$  is an equilibrium if  $u_0 <$   
 216  $w_0$ . If the model starts with  $v = 0$  and  $u$  small everywhere, then the system will tend to stay  
 217 with  $v = 0$ . However, if initially,  $u$  is sufficiently large somewhere, then some  $u$  will switch to

218  $v$ . As the subpopulation with density  $v$  gets concentrated near  $\mu$ , the switching rate might then  
 219 favor further increase in  $v$  and further concentrate the population near  $\mu$ . Modifying the  
 220 movement mechanism to include actual aggregation on the density of conspecifics  
 221 might produce a more concentrated population density on a smaller home range, but it is not  
 222 clear that it can produce home ranging behavior in the absence of other movement components.

223 Scenario 2: Switching Depends on Resource Density. Here, consumers change their movement  
 224 behavior as a function of the density of resources instantaneously available at their immediate  
 225 location. This kind of temporal tracking of resource density is at the heart of the marginal value  
 226 theorem from optimal foraging theory (e.g., Charnov 1976, McNair 1982), but in that case  
 227 (unlike here) such temporal tracking is tied to globally omniscient knowledge of resource  
 228 conditions elsewhere. Assuming a threshold resource density,  $m_0$ , to which the consumers  
 229 respond by switching their movement mode, we write

$$230 \quad \alpha_{s2}(x, t) = \begin{cases} s & \text{if } m(x, t) > m_0 \\ 0 & \text{if } m(x, t) \leq m_0 \end{cases}, \quad (6)$$

231 which means that consumers will switch from random search mode to range resident mode at  
 232 rate  $s$  if the resource density and position  $x$  and time  $t$  exceeds a threshold value,  $m_0$ , and will  
 233 otherwise remain in random search mode. Similarly,

$$234 \quad \beta_{s2}(x, t) = \begin{cases} 0 & \text{if } m(x, t) > m_0 \\ s & \text{if } m(x, t) \leq m_0 \end{cases}, \quad (7)$$

235 such that consumers will switch from range residency to random search mode at rate  $s$  as  
 236 resource availability deteriorates below the threshold density. Note that the structure of  
 237 Equations (6-7) effectively creates an aggregative response to areas of abundant resources.

238 Scenario 3: Switching Depends on Spatial Changes in Resource Density. Whereas Scenario 2  
 239 focused on resource density *per se*, in this scenario, consumers change their movement behavior

240 as a function of the magnitude of the spatial gradient in the resources available,  $\left| \frac{\partial m(x,t)}{\partial x} \right|$ . We

241 write

$$242 \quad \alpha_{S3}(x, t) = \begin{cases} s & \text{if } \left| \frac{\partial m(x,t)}{\partial x} \right| > \varphi_0 \\ 0 & \text{if } \left| \frac{\partial m(x,t)}{\partial x} \right| \leq \varphi_0 \end{cases}, \quad (8)$$

243 where the rate of switching is  $s$  if the spatial gradient in resource availability is greater than the

244 threshold magnitude  $\varphi_0$ , and zero otherwise. Similarly,

$$245 \quad \beta_{S3}(x, t) = \begin{cases} 0 & \text{if } \left| \frac{\partial m(x,t)}{\partial x} \right| > \varphi_0 \\ s & \text{if } \left| \frac{\partial m(x,t)}{\partial x} \right| \leq \varphi_0 \end{cases}, \quad (9)$$

246 such that consumers will switch from range residency to random search mode at rate  $s$  as the

247 spatial gradient in resource availability weakens.

248 Scenario 4: Switching Depends on Perceived Spatial Changes in Resource Density. Here,

249 consumers again change their movement behavior as a function of the spatial gradient in the

250 resources available, but we augment their perceptual abilities to detect those spatial gradients.

251 Specifically, we assume that the consumers possess a perceptual range,  $R$  (Zollner and Lima

252 1997, Mech and Zollner 2002, Fagan et al. 2017). Thus, for a distance  $|x - y|$  from position  $x$  the

253 consumers can perceive the existence of resources according to a detection function

$$254 \quad g(x, y, R) = \begin{cases} 1 & -R \leq x - y \leq R \\ 0 & \text{else} \end{cases}. \quad (10)$$

255 The perceived resource function,  $h(x)$ , is then written

$$256 \quad h(x, t) = \frac{1}{2R} \int_{x-R}^{x+R} \overbrace{m(y, t)}^{\text{available resources}} \overbrace{g(x, y, R)}^{\text{detection function}} dy$$

257 which in the case of  $g(x, y, R)$  from Eq. 10 simplifies to

258 
$$h(x, t) = \frac{1}{2R} \int_{x-R}^{x+R} m(y, t) dy \quad (11)$$

259 We make these choices of  $g(x, y, R)$  and  $h(x)$  to simplify comparisons with the other scenarios  
 260 developed in this paper. The consequences of choosing different functional forms for  $g(x, y, R)$   
 261 are explored extensively in Fagan et al. (2017).

262 To model the effects of switching movement modes as a function of perceived spatial resource  
 263 gradients, we write

264 
$$\alpha_{S4}(x, t) = \begin{cases} s & \text{if } \left| \frac{\partial h(x, t)}{\partial x} \right| > \varphi_0 \\ 0 & \text{if } \left| \frac{\partial h(x, t)}{\partial x} \right| \leq \varphi_0 \end{cases}, \quad (12)$$

265 where the rate of switching is  $s$  if the spatial gradient in resource availability is greater than the  
 266 threshold magnitude  $\varphi_0$ , and zero otherwise. Similarly,

267 
$$\beta_{S4}(x, t) = \begin{cases} 0 & \text{if } \left| \frac{\partial h(x, t)}{\partial x} \right| > \varphi_0 \\ s & \text{if } \left| \frac{\partial h(x, t)}{\partial x} \right| \leq \varphi_0 \end{cases}, \quad (13)$$

268 such that consumers will switch from range residency to random search mode at rate  $s$  when the  
 269 spatial gradient in resource availability is sufficiently weak. Note that because of our choices of  
 270  $g(x, y, R)$  and  $h(x, t)$  in Eqs. 10-11 we can use the same threshold magnitude,  $\varphi_0$ , in Eqs. 12-13  
 271 as in Scenario 3 (Eqs. 8-9).

272 *Scenario 5: Switching Depends on Temporal Changes in Resource Density.* In this penultimate  
 273 scenario, we depart from the previous two scenarios that focused on reaction to spatial gradients,  
 274 and instead assume that the consumers have some modest ability to detect and respond to  
 275 temporal changes in resource density at their specific spatial location (e.g., Loiselle and Blake  
 276 1991, Dusenberry 1998). The assumptions in this scenario of our model mean that consumers  
 277 are able to identify whether their access to immediately local resources is instantaneously getting  
 278 better or worse, but they have no knowledge of long-term trends in resource availability nor any

279 information about trends beyond their current location. Mathematically, we can write this  
 280 detection of immediate trends in terms of the temporal gradient of the resource,  $\frac{\partial m}{\partial t}$ , such that

$$281 \quad \alpha_{S5}(x, t) = \begin{cases} s & \text{if } \frac{\partial m(x,t)}{\partial t} > \delta_0 \\ 0 & \text{if } \frac{\partial m(x,t)}{\partial t} \leq \delta_0 \end{cases}, \quad (14)$$

282 where the rate of switching is  $s$  if the temporal gradient in resource availability is greater than the  
 283 threshold magnitude  $\delta_0$ , and zero otherwise. This means that the consumers only switch from  
 284 random search mode into range resident mode if resource density is improving sufficiently  
 285 quickly. Note that we must use a different threshold,  $\delta_0$ , and not  $\varphi_0$ , because we are dealing with  
 286 a temporal rather than a spatial gradient in resource density. However, because of our choices of  
 287  $m(x, t)$  and  $g(x, t)$ , we can, under some circumstances, use the same magnitude for these  
 288 thresholds and just allow the dimensional units to differ. More specifically, because the resource  
 289 equation for  $m(x, t)$  (and by extension for  $h(x, t)$ ) has a natural time scale of  $4 \pi / \omega$  and a  
 290 natural spatial scale of  $\sigma$  built into it (Eq. 1), we can equate the thresholds  $\delta_0$  and  $\varphi_0$  if we  
 291 equate the magnitudes of the two intrinsic scales. With different choices for these intrinsic scales,  
 292 we can make the same transition from spatial to temporal gradients with a rescaling coefficient.

293 Scenario 6: Switching Depends on Consumers' Memory of Resource Density. Here, we assume  
 294 that the consumers possess a simple, but spatially detailed form of memory that allows them to  
 295 keep track of the long-term resource dynamics of an area. If we were building models of  
 296 movement trajectories for individual animals, we would want to structure each consumer's  
 297 memory around the resources encountered along those trajectories (Schlaegel and Lewis 2014,  
 298 Bracis et al. 2015, Abrahms et al. 2019, Lin et al. 2020). However, because we are working  
 299 within a PDE modeling framework, and need to characterize the collective memory of a group of  
 300 organisms, we need a different approach.

301 To do this, we consider a situation in which the consumers base their decisions to switch  
 302 between movement modes on how much they can remember of the resource cycle and where  
 303 they are within that cycle. From Equation (1), the temporally dynamic resource has period  $1/\omega$   
 304 and repeats endlessly for any given spatial location. We use the parameter  $Q$ , where  $Q \leq 1/\omega$ , to  
 305 represent the memory length, i.e.,  $Q\omega$  is the proportion of the full resource cycle that the  
 306 consumers can remember. The consumers' memory,  $M$ , of the resource conditions leading up to  
 307 time  $t$  can thus be written

$$M = \frac{\int_{t-Q}^t m(x,t) dt}{Q} . \quad (16)$$

309 Note that a given value of  $Q$  will yield a different memory depending on what point in the  
 310 resource cycle the system is in. We then base the movement switching rates on this memory by  
 311 writing

$$\alpha_{S6}(x, t) = \begin{cases} s & \text{if } M > M_0 \\ 0 & \text{if } M \leq M_0 \end{cases} , \quad (17)$$

313 where the rate of switching is  $s$  if the consumers' memory of resource availability at location  $x$   
 314 exceeds the threshold magnitude  $M_0$ , and zero otherwise. This means that the consumers only  
 315 switch from random search mode into range resident mode if their memory of a location, at a  
 316 particular time, is sufficiently positive. Similarly,

$$\beta_{S6}(x, t) = \begin{cases} 0 & \text{if } M > M_0 \\ s & \text{if } M \leq M_0 \end{cases} , \quad (18)$$

318 such that consumers switch from range-resident mode into random search mode if their memory  
 319 of a location, at a particular time, is sufficiently unfavorable, but remain in range resident mode  
 320 otherwise.

### 321 Summary of Modeling Effort

322 Table 1 provides a summary of the different scenarios and the functions and parameters  
 323 involved.  
 324  
 325 Table 1. Summary of the six modeling scenarios and a listing of functions and parameters.  
 326 Scenarios are listed in a 2 x 3 array that matches the presentation style of figures in Results.  
 327 Entries are to be read as “Switching depends on ...”.

**Scenario Summary**

<b>Scenario 1</b> ... conspecific density	<b>Scenario 2</b> ... resource density	<b>Scenario 3</b> ... spatial gradient of resource
<b>Scenario 4</b> ... perceived spatial gradient of resource	<b>Scenario 5</b> ...temporal gradient of resource	<b>Scenario 6</b> ... memory of resource

**Function Summary**

$m(x, t)$	Spatiotemporal distribution of resources
$v(x, t)$	Population density engaged in diffusive movement
$u(x, t)$	Population density engaged in range-resident movement
$\alpha(x, t)$	Rate of switching from diffusive to range-resident movement
$\beta(x, t)$	Rate of switching from range-resident to diffusive movement
$g(x, y, R)$	Resource detection function for foragers with perceptual range $R$
$m(x, t)$	Perceived spatiotemporal distribution of resources

**Parameter Summary**

$\mu$	Mean of the Gaussian resource pulse
$\sigma$	Standard deviation of the Gaussian resource pulse
$\omega$	Temporal frequency of the Gaussian resource pulse
$D$	Diffusion rate
$\varepsilon$	Small background rate of random movement in range-resident movement mode
$\theta$	Rate of home-ranging (mean-reverting) movement
$s$	Rate of switching between diffusive and range-resident movement modes

$w_0$	Threshold forager density determining whether switching of movement modes occurs in Scenario 1
$m_0$	Threshold resource density determining whether switching of movement modes occurs in Scenario 2
$\varphi_0$	Threshold resource gradient determining whether switching of movement modes occurs in Scenarios 3 and 4
$\delta_0$	Threshold temporal resource gradient determining whether switching of movement modes occurs in Scenario 5
$M_0$	Threshold memory of available resources determining whether switching of movement modes occurs in Scenario 6
$R$	Perceptual range in Scenario 4
$M$	Integrated memory of resources in Scenario 6
$Q$	Memory duration in Scenario 6
$\Omega$	Degree of spatiotemporal matching between foragers and their resources

328

329 Quantifying Foraging Success To quantify the consumers' ability to track the distribution of  
330 their resources over space and time, we use the continuous form of the Bhattacharyya Coefficient  
331 (BC; Bhattacharyya 1943) for quantifying the overlap between two distributions. Because the  
332 BC was initially formulated for use with probability distributions, we use a normalized form.  
333 Specifically, we have

$$334 \quad \Omega = \frac{\int_{t'}^{t_{max}} \int_0^{100} \sqrt{[u(x,t)+v(x,t)]m(x,t)} dx dt}{\sqrt{\int_{t'}^{t_{max}} \int_0^{100} [u(x,t)+v(x,t)] dx dt} \sqrt{\int_{t'}^{t_{max}} \int_0^{100} m(x,t) dx dt}} \leq 1 \quad . (19)$$

335 The timeframe  $t'$  to  $t_{max}$  represents some period after transient behaviors have settled down.

336 For static resource distributions, which (with appropriate boundary conditions of mass  
337 conservation) always exhibit an equilibrium solution, the integral is only over space (Fagan et  
338 al. 2020). For dynamic landscapes, such as periodically fluctuating landscapes on which we  
339 focus, the time integral needs to be taken over a long enough period to discount the transient

340 behaviors and instead capture long-term variation (Fagan et al. 2017). This metric of foraging  
341 success differs a bit from that used in Fagan et al. (2017, 2020), but the change is necessary to  
342 accommodate comparison across all six of the scenarios we consider here.

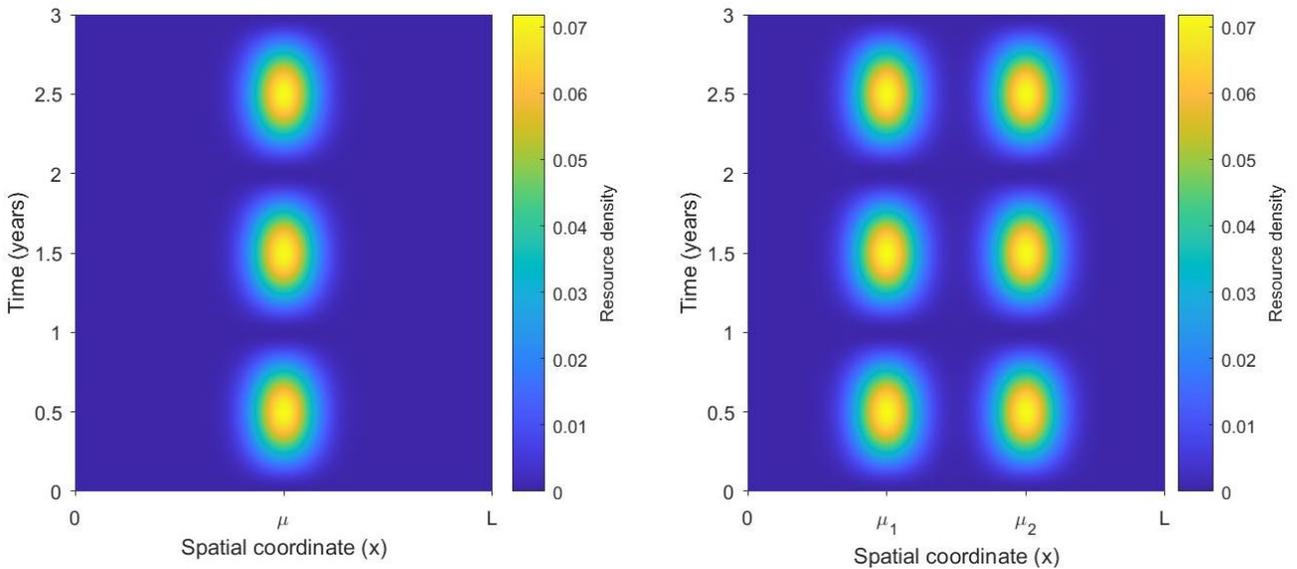
343 Equation (19) quantifies ‘resource matching’ in the sense that foragers must spatially and  
344 temporally overlap with resources to be successful. We do not consider mutual interference or  
345 resource depletion because we want to focus only on animal movement behavior and not  
346 population growth or decay. This is a reasonable assumption when population density is low  
347 (i.e., sparsely populated regions) and resources are ephemeral (i.e., resources degrade before  
348 their density can be reduced much by the foragers). In these systems, the question is more about  
349 capitalizing on transient resources, as opposed to avoiding competition. Such transient resource  
350 dynamics characterize, for example, the Eastern steppes of Mongolia that have motivated much  
351 earlier work on animal movement (Mueller and Fagan 2008, Mueller et al. 2011, Martínez-  
352 Garcia et al. 2013, Fleming et al. 2014).

353 Throughout, we solved the initial-boundary value problem numerically using the method  
354 of lines by discretizing in space over the domain  $x = [0, 100]$  and solving the system of ordinary  
355 differential equations in time. We implemented a different scheme for the components of Eq. 2  
356 as required by their respective structure. For example, for the random search equation, we used a  
357 simple forward-time, centered-space scheme, whereas for the gradient following equation, we  
358 used the Lax-Wendroff method, accounting for the method’s natural dispersion error in the term  
359  $\varepsilon \frac{\partial^2}{\partial x^2} v$ . To solve the resulting coupled system of ODEs, we used the variable-step, variable-order  
360 differential algebraic equation solver ODE15S (Shampine and Reichalt, 1997).

361 For initial conditions, all the numerical experiments had  $u$  and  $v$  distributed uniformly  
 362 with population density  $1 / L$ . Thus, at any time the total population  $u + v$  would integrate to 2  
 363 over space, while the total population in the individual  $u$  and  $v$  components varied with time. We  
 364 used zero flux boundary conditions on the rectangular domain  $(x, t) \in [0, 100] \times [0, \infty)$ . For all of  
 365 the simulations, we considered the pulsed Gaussian resource function detailed in Eq. 1.

366 RESULTS

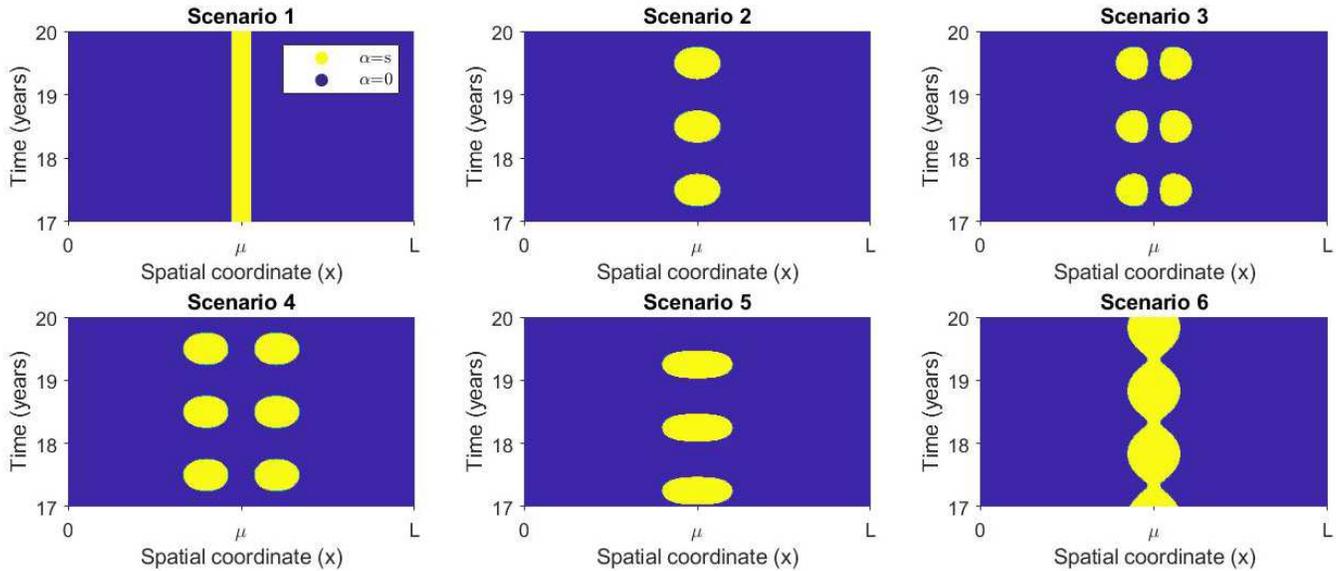
367 Figure 1 shows the dynamic (pulsed Gaussian) resource landscapes on which the forager  
 368 populations are moving. In both the single patch and two patch landscapes, resources are highly  
 369 transient but are predictable with regard to their location and timing.



371 Figure 1. Heatmaps of the resource landscapes with one (left) and two (right) seasonally pulsed  
 372 Gaussian resource peaks. Note that the variations in the resources are sufficiently intense that the  
 373 resource density drops to near zero during the troughs between the resource peaks. Parameters:  $L$   
 374  $= 100$ ,  $\mu = 50$ ,  $\mu_1 = 33.3$ ,  $\mu_2 = 66.6$ ,  $\sigma = 5.5$ ,  $\omega = 0.2$ .

375  
 376 The six advection scenarios involve starkly different locations and times at which the  
 377 consumers are switching from the diffusive foraging mode to the home ranging mode (Figure 2).  
 378 For example, in Scenario 1, switching into the home ranging mode is constant after the

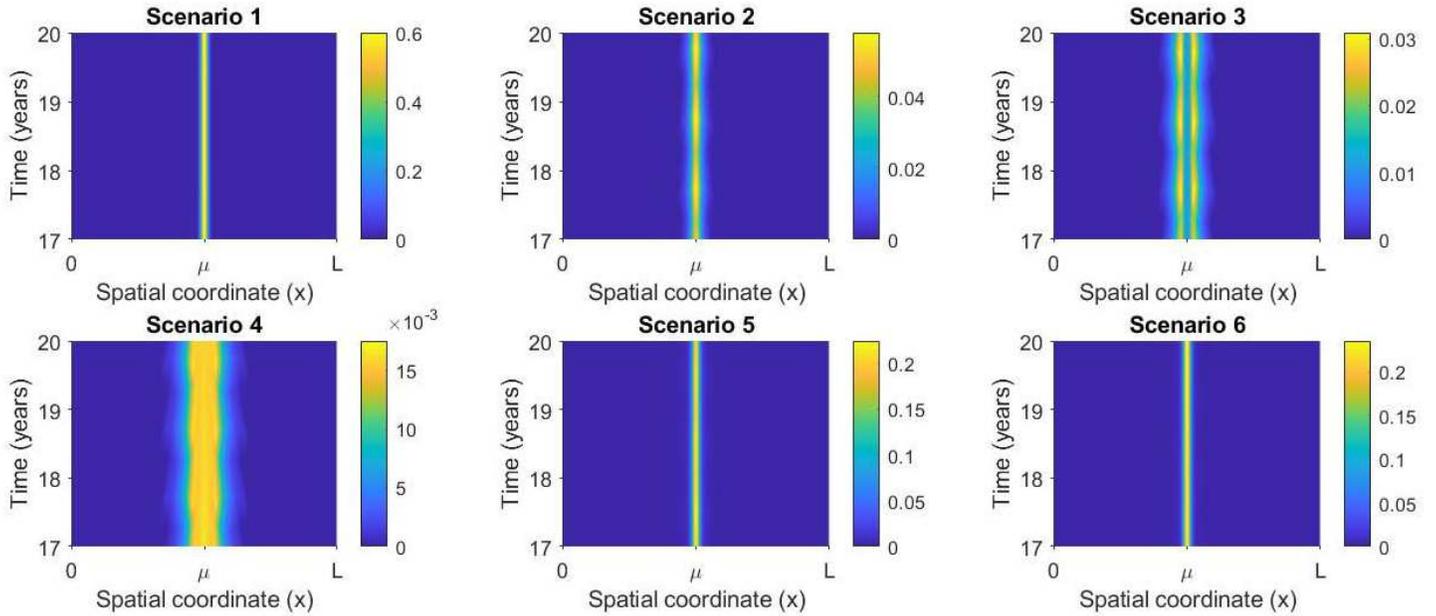
379 population equilibrates, with no influence from the underlying periodicity in resource  
380 availability. In contrast, the resource conditions that favor switching to home ranging are  
381 strongest at the time and location of the resource peak in Scenario 2 (tracking the resource  
382 density, Fig. 2 b) whereas the resource conditions that favor switching are strongest on the  
383 ‘shoulders’ of the resource peak in Scenarios 3 and 4 (tracking changes and perceived spatial  
384 changes in resource density, respectively) (Fig. 2c,d). Provided  $R$  in Equation 10 (perception  
385 scenario) is sufficiently small, the resource conditions favoring switching regions for scenario 4  
386 are nearly identical to those of scenario 3 for low  $R$  (Supp. Fig. F). Different still are the resource  
387 conditions that promote the switching behavior in Scenario 5 (tracking temporal changes in  
388 resource density) where the switching behavior is greatest as the resource begins to increase in  
389 density (Fig. 2e). Provided  $Q$  in Eq. 16 (memory scenario) is sufficiently large, resource  
390 conditions will lead to some portion of the consumer population constantly switching into the  
391 diffusive foraging mode regardless of what part of the seasonal cycle the system is in (Fig. 2f).  
392 In contrast, for sufficiently small  $Q$ , the resource conditions promoting this constancy of  
393 switching disappears and the results from Scenario 6 converge on those from Scenario 2 (Supp.  
394 Fig. G). Resource conditions that promote switching from home ranging to diffusive foraging  
395 mode are largely complementary to these results for all six scenarios for switching from diffusive  
396 to home ranging.



398  
 399 **Figure 2.** Location and timing of the resource conditions that promote the consumer population  
 400 actively switching into home ranging mode for the landscape with a single resource patch (see  
 401 Fig. 1a). Note how the intensity of the resource conditions that promote switching behavior as  
 402 well as the timing and location of those favorable locations vary strongly depending on how the  
 403 gradient of the resource is defined (labeled as scenarios 1 – 6). Fixed parameters:  $\theta = 0.01$ ,  $D =$   
 404  $0.1$ ; Scenario 1:  $\theta = 0.01$ ,  $D = 0.1$ ,  $w_0 = 0.01$ ; Scenario 2:  $m_0 = 0.035$ ; Scenario 3:  $\varphi_0 = 0.0037$ ;  
 405 Scenario 4:  $\varphi_0 = 0.0018$ ,  $R = 10$ ; Scenario 5:  $\delta\theta = 0.0014$ , Scenario 6:  $M_0 = 0.02$ ,  $Q = 20.9$ .

406  
 407 The differences in switching behavior among Scenarios alter the consumers' movement  
 408 behaviors and thus translate into differences in the location and timing of the consumer  
 409 population densities. Scenario 1 (tracking conspecific density) shows a concentration of  
 410 consumers to the location of the resource peak regardless of whether the resource is at high or  
 411 low density. In contrast, Scenario 2 (tracking resource density) shows periodicity in the  
 412 consumer population density, indicating a degree of matching of the consumers to both the  
 413 location and timing of the resource peak. Scenario 3 (tracking spatial changes in resource  
 414 density) shows the consumers concentrating on the shoulders of the resource peak, but not on the  
 415 resource peak itself. In contrast, scenario 4 (tracking perceived spatial changes in resource  
 416 density) shows advection occurring over a much broader area. In scenarios 5 (tracking temporal

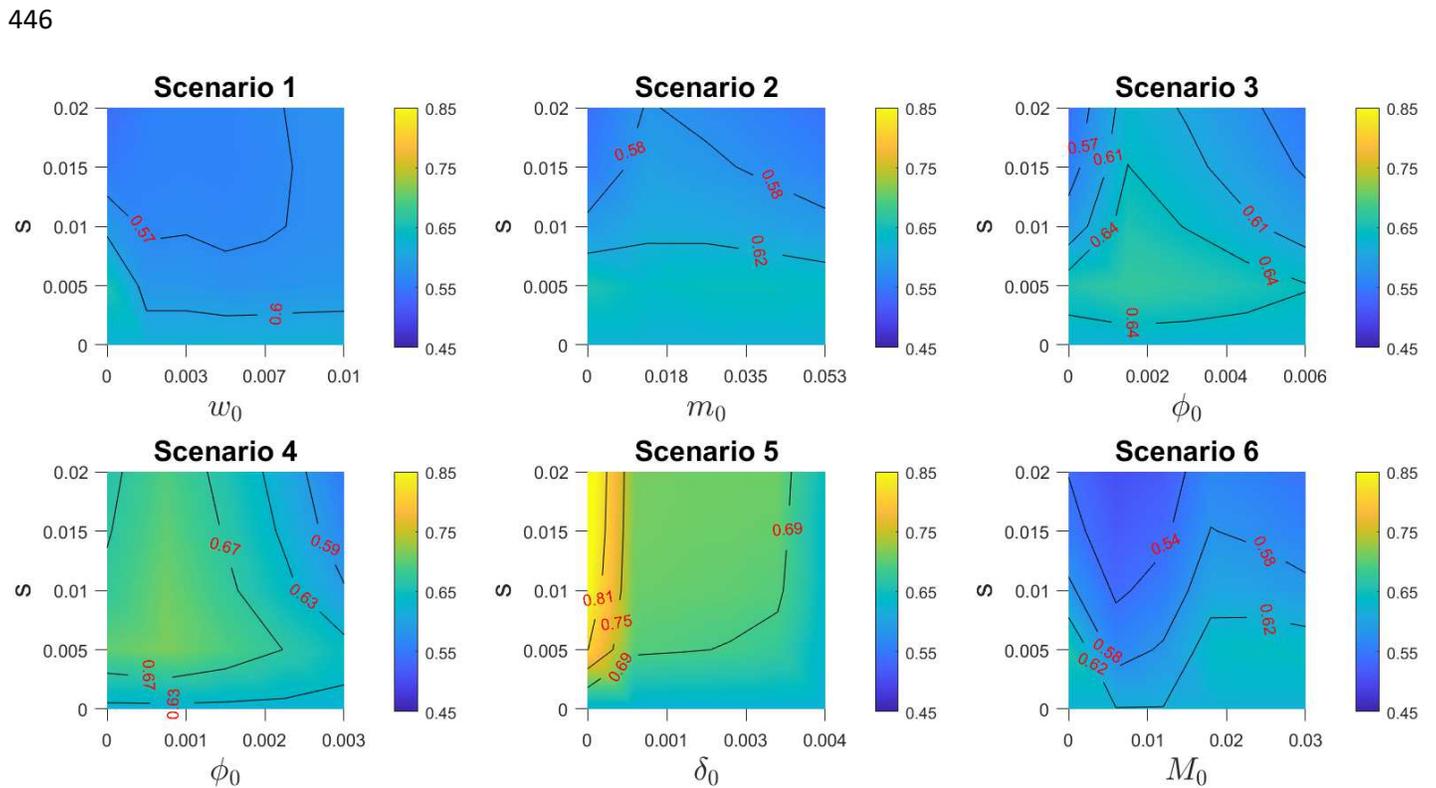
417 changes in resource density) and 6 (memory), the density of the advecting consumers is greatest  
 418 on the resource peak. Both of these scenarios also feature a limited degree of oscillation in  
 419 population density that mirrors the temporally dynamic nature of the resources. Supplementary  
 420 Figure A provides the corresponding densities for the diffusive component of the populations.  
 421



423  
 424 Figure 3. Densities of the home ranging component of the consumer population across the six  
 425 switching scenarios for the landscape with a single resource peak. Scenarios differ with regard to  
 426 both the timing and location of the density of the portion of the consumer population that is in  
 427 the home ranging mode. Note that densities fluctuate strongly in time in Scenarios 2 and 3. Note  
 428 also that densities are concentrated on the ‘shoulders’ of the resource distribution in Scenario 3  
 429 and over a much broader area in Scenario 4. Fixed parameters:  $\theta = 0.01$ ,  $D = 0.1$ ; Scenario 1:  
 430  $w_0 = 0.01$ ; Scenario 2:  $m_0 = 0.035$ ; Scenario 3:  $\varphi_0 = 0.0037$ ; Scenario 4:  $\varphi_0 = 0.0018$ ,  $R = 10$ ;  
 431 Scenario 5:  $\delta_0 = -0.0014$ , in Scenario 6  $M_0 = 0.02$ ,  $Q = 20.9$ .

432  
 433 In the case of a single resource patch, considerable differences exist in  $\Omega$  across  
 434 scenarios, indicating that the different movement strategies allow for very different degrees of  
 435 resource matching. Resource matching success ( $\Omega$ ) is clearly greatest in Scenario 5 where  
 436 switching between diffusive and home ranging movement types depends on the temporal  
 437 resource gradient, but only when the threshold for switching between movement behaviors is

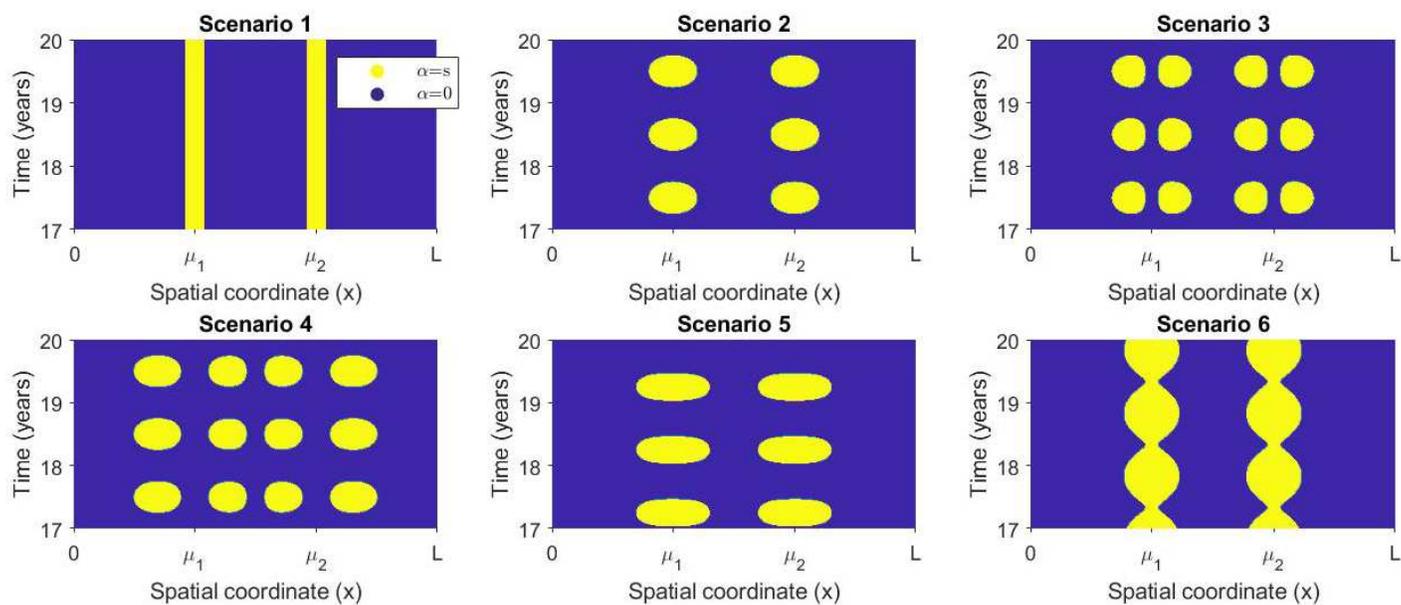
438 very small (Figure 4). Peak  $\Omega$  values (broad to concentrated in parametric extent) exist within  
 439 each scenario, and the location of these  $\Omega$  peaks differs across scenarios. Collectively, these  
 440 results indicate that, within a given movement strategy, resource matching could potentially be  
 441 optimized, but that the degree of switching and the switching thresholds that are necessary to  
 442 provide optimal matching differs among scenarios. For example, in Figure 4, low levels of  
 443 switching provide marginally better resource matching in Scenarios 1 and 2, but switching needs  
 444 to occur at a faster rate when it occurs in conjunction with temporal resource gradients (Scenario  
 445 5).



448  
 449 Figure 4. Resource matching success ( $\Omega$ ) for foragers in a landscape with a single periodic  
 450 resource peak. Results for all scenarios are plotted as functions of switching rates (x axes) and  
 451 scenario-specific parameters (y-axes). Fixed parameters  $\theta = 0.01$ ,  $D = 0.1$ : Scenario 4:  $R=10$ ;  
 452 Scenario 6:  $Q=20.9$ .

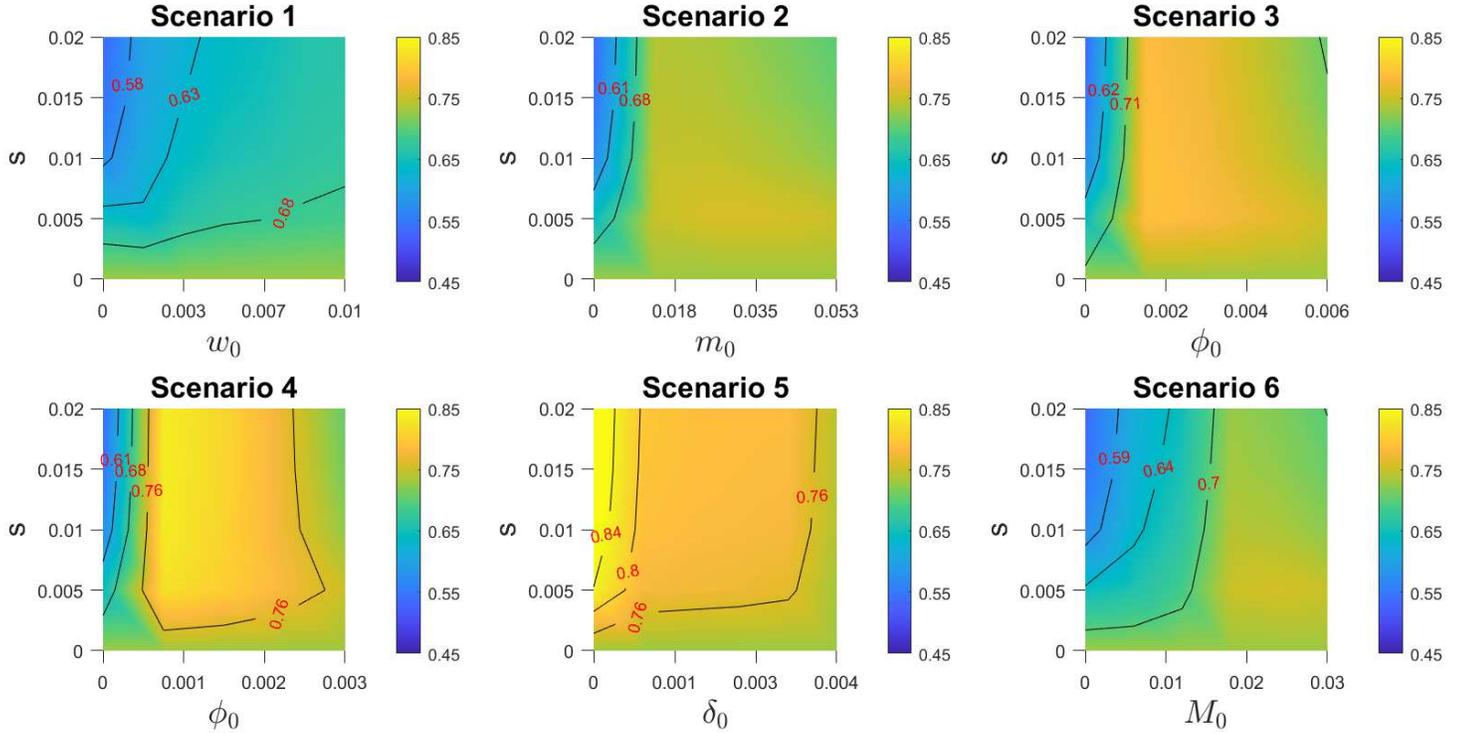
453  
 454

455           In the case of two resource patches, the location and timing of the consumer population  
456 switching into home ranging mode becomes more complicated, reflecting the greater complexity  
457 of the resource conditions favoring such changes in behavior (Figure 5). The timing and location  
458 of such switching vary strongly across scenarios depending how the gradient of the resource is  
459 defined. For example, switching to advection is consistently concentrated in the vicinity of the  
460 resource peaks in Scenario 1 even though the resource is periodic in time. Switching to advection  
461 occurs on the ‘shoulders’ of the double-peaked resource distributions in Scenarios 3 and 4, but  
462 occurs in the vicinity of, but in advance of, the resource peaks in Scenario 5 (excluding only the  
463 spatiotemporal region where the resource is most strongly waning in abundance). In Scenario 6,  
464 switching to advection again reflects the periodic nature of the resource, but, due to the effects of  
465 memory, there exists a lingering degree of switching near the centers of the resource peaks even  
466 though the resources are least abundant at these times (Figure 5). Density plots for the  
467 component of the consumer population in the home ranging mode appear in Supplementary  
468 Figure B. A counterpart to Figure 5 that shows the location and timing of the population  
469 switching from foraging mode into diffusive mode appears in Supplementary Figure C.  
470



472 **Figure 5.** Location and timing of the consumer population switching into home ranging foraging  
 473 mode for the landscape with two in-phase resource peaks (see Fig. 1b). Compare results with  
 474 Figure 2. Fixed parameters:  $\theta = 0.01$ ,  $D = 0.1$ ; Scenario 1:  $w_0 = 0.01$ ; Scenario 2:  $m_0 = 0.035$ ;  
 475 Scenario 3:  $\varphi_0 = 0.0037$ ; Scenario 4:  $\varphi_0 = 0.0018$ ,  $R = 10$ ; Scenario 5:  $\delta_0 = 0.0014$ ; Scenario 6  $M_0$   
 476  $= 0.02$ ,  $Q = 20.9$ .

477  
 478 Compared to Figure 4, resource matching success is generally higher in the two patch  
 479 case because the resources are better distributed within the landscape and easier to find with a  
 480 given level of mobility (Figure 6). This is especially true for Scenario 3 (spatial gradient) and  
 481 Scenario 4 (spatial gradient with non-local perception) where resource matching success is now  
 482 on par with the best performing parameters from Scenario 5 (following a temporal resource  
 483 gradient). High levels of switching between diffusion and advection are generally deleterious  
 484 unless the thresholds for undertaking such switches are sufficiently high. The thresholds at  
 485 which optimal resource matching is reached tend to be higher in this two resource patch case  
 486 than in the single resource patch.



488 Figure 6. Resource matching in the case of two in-phase resource patches. Compare results with  
 489 Figure 4. Fixed parameters  $\theta = 0.01$ ,  $D = 0.1$ : Scenario 4:  $R=10$ ; Scenario 6:  $Q=20.9$ .

490

491 The home ranging parameter,  $\theta$ , also influences the degree of resource matching success.

492 Supplementary Figure D gives resource matching success in the case of one resource path

493 (comparable to Figure 4), except that  $\theta$  is increased and, separately, decreased from the baseline

494 level. For a fixed rate of diffusion, increasing  $\theta$  affords greater resource matching success for

495 almost all scenarios and decreasing  $\theta$  has the opposite effect. Scenario 1 (advection on

496 conspecifics) clearly differs in that increasing  $\theta$  leads to a decrease in resource matching. For the

497 case of two resource peaks (Supp. Figure E, compare with Fig. 6),  $\theta$  has a different effect in that

498 increasing the degree of home ranging tends to decrease  $\Omega$ , at least somewhat, except in

499 Scenarios 3 and 4. In these scenarios, where the behavioral switching depends upon a form of

500 spatial resource gradient, resource matching clearly increases with increasing  $\theta$ .

501           Perceptual range ( $R$ ) plays an important role in the degree of resource matching success  
502 afforded by Scenario 4 by shifting the timing and location of the behavioral switching into the  
503 home ranging mode (Supplementary Figure F). For sufficiently small  $R$ , results from Scenario 4  
504 converge on those of Scenario 3. For sufficiently large  $R$ , the switching regions become more  
505 refined as the organisms' increased perceptual radius affords more information on the full  
506 distribution of resources across the domain and the ideal times and locations to switch behaviors.  
507 Note that for  $R=15$ , which is exactly half the distance between the centers of the two resource  
508 pulses, the switching regions turn on and off centered at  $x = 50$  (Supplementary Figure F).

509           Likewise, the duration of memory in Scenario 6 can also influence the timing and  
510 location of behavioral switching (Supplementary Figure G). As memory duration,  $Q$ , increases,  
511 the lingering effects of memory tend to link the switching responses to consecutive resource  
512 peaks so that switching to advection occurs in a consistent location, even though the underlying  
513 resource is periodic in time. For sufficiently small  $Q$ , switching behavior of Scenario 6 converges  
514 on that of Scenario 2.

## 515 **DISCUSSION**

516           This synthetic overview makes clear that the ecological concept of 'consumers tracking  
517 resource gradients' can mean very different things in practice when implemented in movement  
518 models with continuous space. Furthermore, the detailed assumptions of how consumers actually  
519 track their resources can translate into radically different levels of success for consumers  
520 attempting to match the spatiotemporal distributions of their resources.

521           Overall, we found that Scenarios 3 (tracking spatial gradients), 4 (tracking spatial  
522 gradients with the benefit of non-local perception), and 5 (tracking temporal gradients) provided  
523 the highest level of resource matching for consumers. To some extent these advantages may

524 change with the distribution of resources. For example, if one considers a resource distribution  
525 function which is very flat around its global maximum point but peaked around a local maximum  
526 point, Scenario 3 would likely provide very poor resource matching levels. In this scenario,  
527 tracking perceived spatial gradients (Scenario 4) should perform better than tracking the  
528 immediately local gradients (Scenario 3). Results in Fagan et al. (2020), where we considered  
529 step functions for the resources, support this contention. Perception (Scenario 4) afforded good  
530 resource matching success, comparable to the highest levels of resource matching that were  
531 obtained through Scenario 5 (tracking temporal gradients). The utility of perception, which was  
532 especially true in more complex two patch resource landscapes, is in line with earlier studies  
533 suggesting the benefits of non-local information gathering in temporally variable resource  
534 landscapes (Fagan et al. 2017).

535         The general superiority of Scenario 5 (tracking temporal gradients) may be, in part, due  
536 to the mathematical model of movement that we explored. For example, because  $\mu$ , the spatial  
537 location of resources, is built into the range-resident dispersal mode, there is spatial information  
538 built into that mode, but no temporal information. Then, adding temporal information via  
539 tracking of temporal gradients (Scenario 5) would add relatively more to an organism's overall  
540 information about the environment than using additional spatial information, because there is  
541 already some spatial information implicitly available in the OU mode. The observation that  
542 Scenarios 3 and 4, especially 4, perform relatively better when there are two resource patches  
543 than where there is only one supports this argument, because with two resource locations getting  
544 extra spatial information might be more valuable.

545         In contrast to the more successful strategies (Scenarios 3, 4, and 5), other scenarios  
546 involving tracking the density of conspecifics (Scenario 1), tracking the abundance (rather than

547 the gradient) of resources (Scenario 2), or employing a particular form of memory (Scenario 6)  
548 provided poorer spatiotemporal matches to resources. Consumers that switched their foraging  
549 behavior as a function of conspecific densities generally achieved very poor resource-matching  
550 success. The effect was especially pronounced when home ranging behavior was strong, which  
551 limited the consumers' spatial exploration. These results suggest that pure 'local enhancement'  
552 type mechanisms (Buckley 1997) wherein consumers aggregate in areas where others of their  
553 kind are already foraging cannot succeed in isolation. Instead, a modest level of directly tracking  
554 the resources themselves, together with cueing in on conspecific activity, would likely improve  
555 this strategy. This modification would also connect to the producer – scrounger dichotomy in  
556 studies of social group foraging behavior (Beauchamp 2000), wherein 'producers' behave  
557 directly according to resources but 'scroungers' base their decisions on producers.

558         Increasing evidence suggests that memory is important for consumers that must acquire  
559 resources in highly dynamic landscapes (Bracis and Mueller 2017, Abrahms et al. 2020).  
560 Consequently, we were surprised to see that memory-based movement also provided some of the  
561 worst tracking of available resources. This deviation from expectations may stem from the  
562 particular (rather crude) form of memory that we implemented in Scenario 6. Indeed, other  
563 modeling work that considered memory at the individual (rather than collective) level, found that  
564 a rather sophisticated form of memory, including separate long- and short-term memory records,  
565 was necessary to track resources in dynamic landscapes (Lin et al. 2021).

566         Collectively, these results suggest that tracking gradients (Scenarios 3, 4, and 5) may, in  
567 general, be more effective than tracking resource density directly (Scenario 2) or indirectly  
568 (Scenario 1). One plausible reason for this is that gradients should be detectable over a broader  
569 range of conditions than density per se. This would accord with the underlying biology.

570 Consider that, in practice, it would often be easier to assess the gradient of something than its  
571 magnitude. For example, discerning whether movement was up or down a hill would likely be  
572 easier than identifying the elevation. Such differential identifiability of gradients versus  
573 magnitudes would likely hinge on the rate of movement relative to the scale of the gradient.

574 Intriguingly, the different scenarios for switching between home ranging and diffusive  
575 movement did not rank consistently with regard to the level of resource matching that they  
576 afforded. Even something as simple as switching from a model with a single periodic resource  
577 peak to one with two periodic resource peaks changed the relative performance of the different  
578 scenarios for switching between home ranging and random movement (compare Figures 4 and  
579 6). These differences appear to arise, primarily, because changing the number of resource peaks  
580 changes the average location of resources relative to consumers with specific levels of mobility.

581 The degree to which consumers incorporate range-resident behavior in their movement  
582 also played an important role in determining how well they overlap the distribution of their  
583 resources in space and time. In particular, the strength of home ranging (relative to random  
584 dispersal) interacted with the behavioral cues for switching to shape resource overlap in a strong  
585 way. Switching based on spatial resource gradients (whether immediately local or perceived over  
586 a longer distance) provided particularly good matches to resource distributions when coupled  
587 with strong range-resident behavior. This result is intriguing given that a recent statistical  
588 analysis of home range behavior found that many animals' movement patterns were well  
589 described by models that included elements of both diffusive and range-resident behavior  
590 (Noonan et al. 2019).

591 The conditional similarities between Scenarios 3 and 4 (Supp. Fig. F), and separately,  
592 between Scenarios 2 and 6 (Supp. Fig. G), are due to their underlying mathematics. Specifically,

593 the switching functions in Scenarios 2 and 3 were based on a derivative, whereas in Scenarios 4  
594 and 6 the switching functions were based on a slope which approximated the respective  
595 derivative for low enough  $R$  or  $Q$ . In contrast, for large values of  $R$  or  $Q$ , Scenarios 4 and 6  
596 departed strongly from Scenarios 3 and 2, respectively, demonstrating how the introduction of  
597 additional information caused different behavior by the home ranging component of the  
598 population (Supp. Figs. F and G). This additional information may be either spatial (in the form  
599 of an increased perceptual range, Scenario 5) or temporal (in the form of a lingering memory,  
600 Scenario 6), but in either case the additional information altered the basis for the behavioral  
601 decision-making.

#### 602 *Opportunities for optimal resource matching*

603 The existence of parameter regions featuring higher levels of resource matching success  
604 amidst a sea of lower-performing parameters (Figs. 4 and 6, Supp. Figs. D and E) suggests that,  
605 within a given movement strategy, resource matching could potentially be optimized. However,  
606 the rate of switching (between home ranging and diffusive movement modes) and the switching  
607 thresholds that are necessary to provide optimal resource matching differ quite strongly among  
608 scenarios. For example, in Figure 4, low rates of switching provide marginally better resource  
609 matching in Scenarios 1 and 6, but switching needs to occur at a faster rate when it occurs in  
610 conjunction with temporal resource gradients if consumers are to achieve the highest levels of  
611 resource matching (Scenario 5).

612 Although our study considered models with continuous space, the high levels of resource  
613 matching success observed in some scenarios brings to mind concepts like the marginal value  
614 theorem for optimal resource tracking (Charnov 1976, McNair 1982) and the ideal free  
615 distribution for optimal distribution of resources among consumers (Farnsworth and Beecham

616 1999, Křivan et al. 2008) that had their origins in patch-based models of consumers tracking  
617 resources. To our knowledge, there is nothing like the marginal value theorem in partial  
618 differential equation (PDE) models or other ecological models involving continuous space.  
619 However, there is a strong foundation for the ideal-free distribution in continuous space models  
620 (Arditi and Dacorogna 1988, Grunbaum 1988), and more recent PDE work demonstrates how  
621 certain kinds of resource tracking strategies can lead to an ideal free distribution of consumers  
622 (Cantrell et al. 2008, 2010). Real world complications, such as perceptual constraints, can cause  
623 departures from an ideal free distribution (Abrahams 1986), but ‘approximately optimal’  
624 solutions are possible even when underlying assumptions are violated (Griffen 2009, Street et al.  
625 2018).

626         In general, optimal movement in heterogeneous landscapes requires that consumers  
627 consider both space and time (Arditi and Dacorogna 1988, Cantrell et al. 2021). In this paper,  
628 Scenarios 2,3, and 4 consider space, 5 considers time, and 6 considers both space and time (but  
629 considers time, via memory, in a rather crude way). However, all of these scenarios involve  
630 behaviors that are relatively simple, in that movement decisions are being made with respect to  
631 metrics observable by many animals. Of the switching cues we examined, that of Scenario 2 is  
632 closest to classical considerations of optimal foraging in patchy landscapes. From the marginal  
633 value theorem, we know that, for omniscient consumers, the best time to leave a patch is when  
634 the rate of resource uptake on that patch drops below the system-wide average (Charnov 1976).  
635 This criterion reflects elements present in both Scenarios 2 and 5. Scenario 2 is relevant because  
636 resource uptake should be proportional to the density of resources available. However, Scenario  
637 5, where the focus is the temporal rate of change of resource density, is also relevant in that the  
638 rate of change of available resources shapes the rate of resource uptake. For example, knowing

639 the rate of change in resource availability would offer consumers information on how much  
640 longer they have to gather resources. This information could be far more valuable than just  
641 knowing what resources are available at an exact spatiotemporal location. These conceptual links  
642 to the marginal value theorem are particularly strong for cases where behavioral changes are  
643 framed in terms of optimal ‘giving up times’ (McNair 1982) or residence times (Turchin 1991).  
644 Overall, Scenario 5 afforded much better opportunities for resource overlap than did Scenario 2  
645 (Figures 4, 6, Supp. Figs. D, E). This result raises intriguing questions about optimal foraging in  
646 dynamic landscapes, including the possibility that consumers tracking both the rate of change in  
647 local conditions and their own rate of change of resource uptake may be especially adept at  
648 maximizing resource gain. This will be explored in future work. Additional future directions  
649 could include models that combine memory and perception together, or that combine local  
650 enhancement type strategies (Scenario 1) with gradient-following behavior.

651 In summary, we compared the performance of alternative methods by which consumers  
652 can be reasonably said to be tracking gradients related to their resources. Optimal resource  
653 matching is achievable via all six scenarios, at least to some degree. Within most scenarios, a  
654 broad range of parameter values yields similarly high levels of resource matching success. Thus,  
655 even if consumers were channelized to possess particular resource tracking abilities and were  
656 unable to switch among scenarios, wide parametric regions of ‘nearly optimal’ resource  
657 matching success would provide a broad evolutionary target wherein good foraging success is  
658 obtainable even when the parameters cannot be fine-tuned. Such broad targets would be  
659 advantageous given the high degree of temporal resource variability that exists in natural systems  
660 (e.g., Abrahms et al. 2020).

661

662

663 DECLARATIONS

664 i. Funding

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666

667 ii. Conflicts of interest/Competing interests

668 The authors have no conflicts of interest nor competing interests. The authors have no relevant  
669 financial or non-financial interests to disclose.

670

671 iii. Ethics approval

672 Not applicable.

673

674 iv. Consent to participate

675 Not applicable.

676

677 v. Consent for publication

678 Not applicable.

679

680 vi. Availability of data and material

681 Not applicable.

682

683 vii. Code availability

684 Code is available on request from WFF.

685

686 viii. Authors' contributions

687 WFF, RSC and GCC conceived of the original problem. CS and EG helped refine the project. CS  
688 developed the code with assistance from TH and EG. WFF wrote the initial draft and all authors  
689 have edited and revised the text.

690

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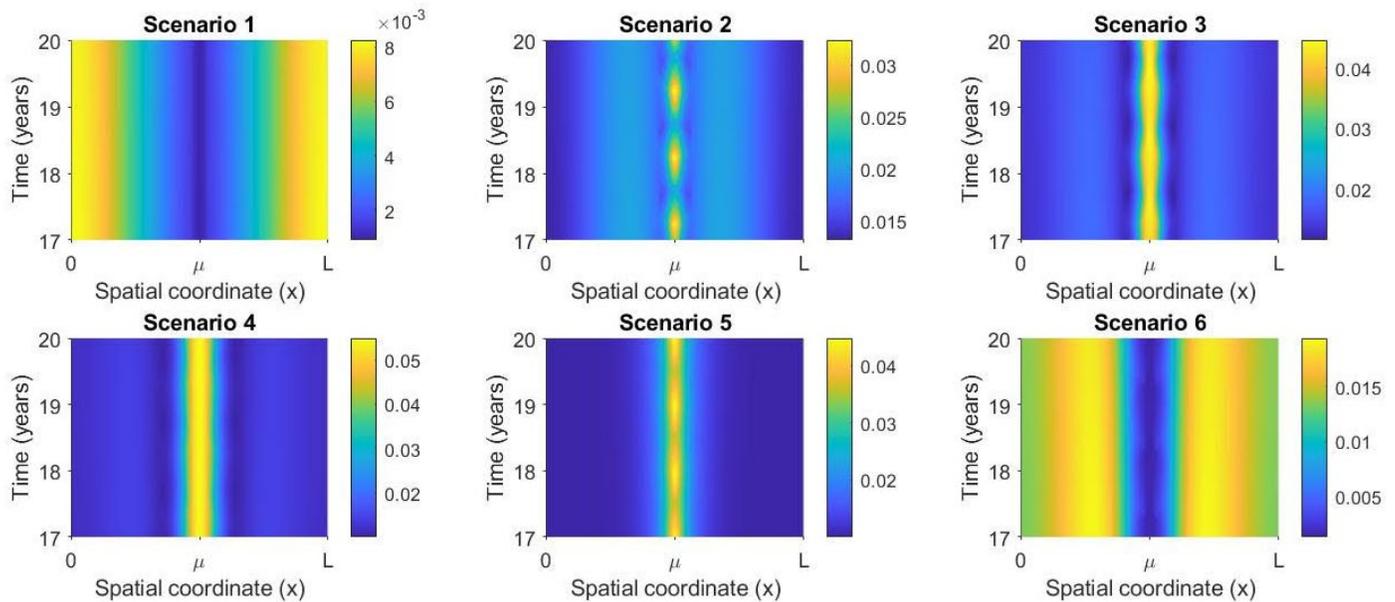
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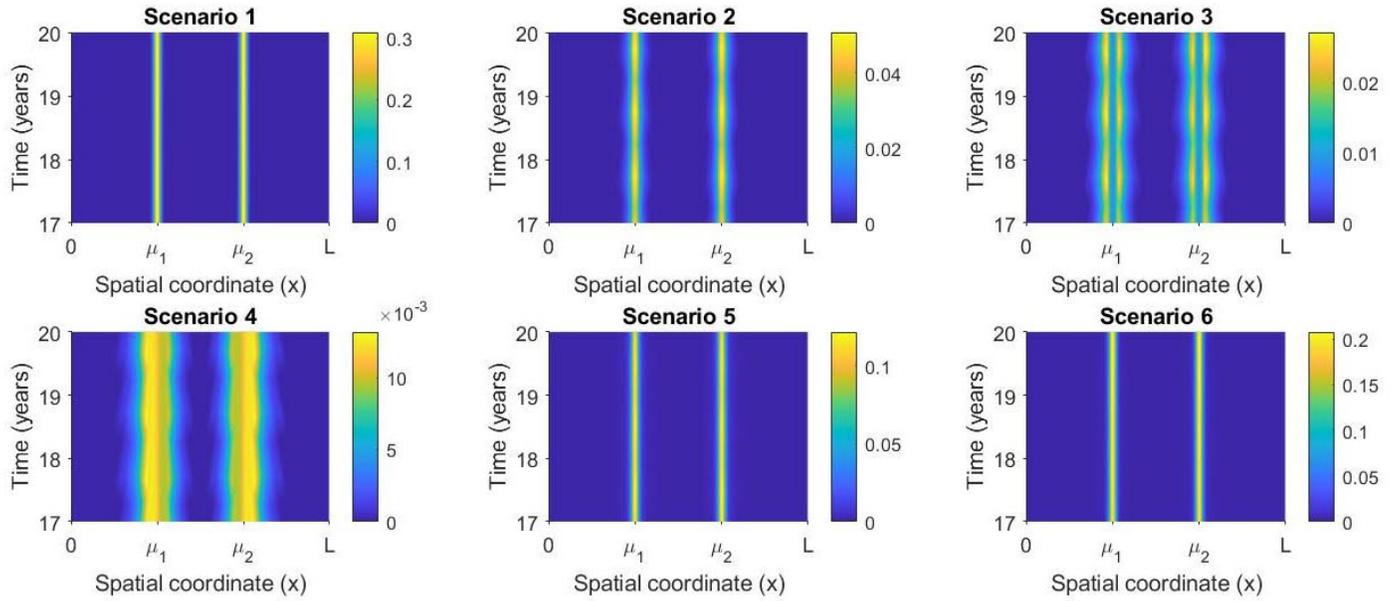
831 **Supplemental Figures.**



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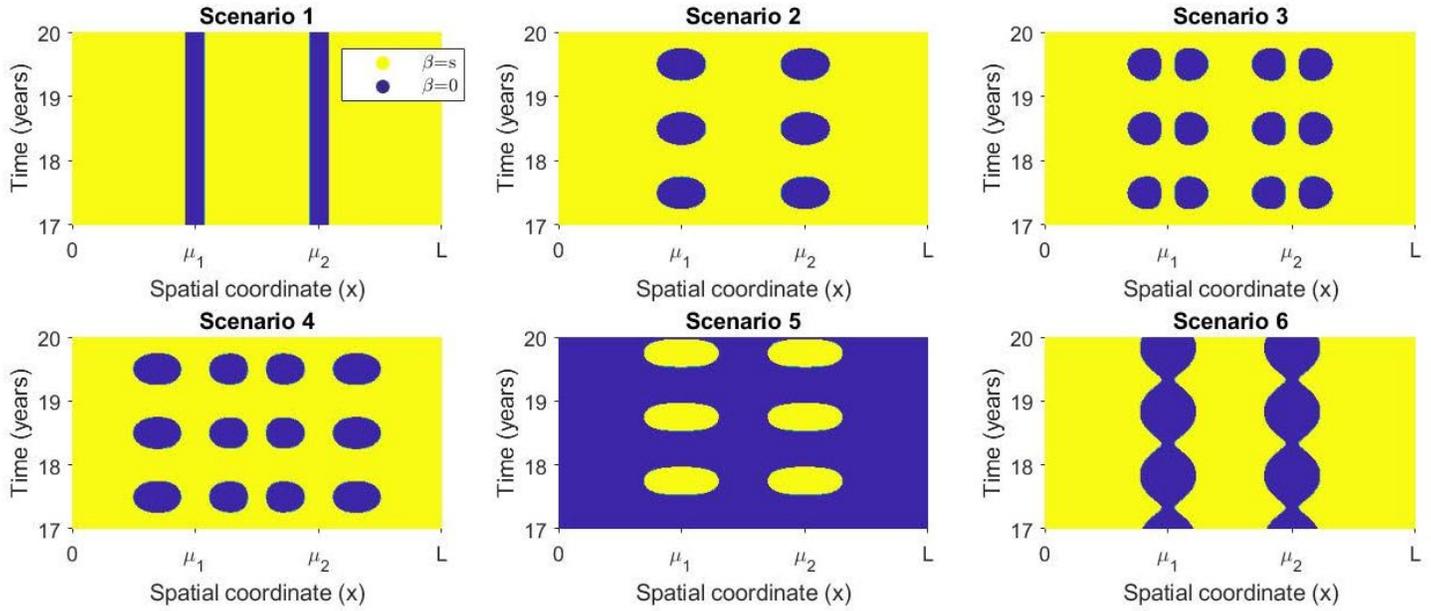
834 Supplementary Figure A. Density plot of the diffusive component of the forager population in a  
835 landscape with a single, periodic resource peak. Diffusion is utilized in very different ways  
836 across the six movement scenarios. For example, large portions of the population are diffusing in  
837 locations away from the resource peak in Scenarios 1 and 6. Diffusion occurs concentrated near  
838 the resource peak in Scenarios 2 through 5, but in a strongly periodic fashion in Scenarios 2 and  
839 5. Fixed parameters:  $\theta = 0.01$ ,  $D = 0.1$ ; Scenario 1:  $w_0 = 0.01$ ; Scenario 2:  $m_0 = 0.035$ ; Scenario  
840 3:  $\varphi_0 = 0.0037$ ; Scenario 4:  $\varphi_0 = 0.0018$ ,  $R = 10$ ; Scenario 5:  $\delta_0 = 0.0014$ ; Scenario 6  $M_0 = 0.02$ ,  
841  $Q = 20.9$ .

842



844 Supplemental Figure B. Densities of the home ranging component of the population for a  
 845 landscape with two in-phase resource patches. Compare with Figure 3 for the one resource patch  
 846 case. Fixed parameters:  $\theta = 0.01$ ,  $D = 0.1$ ; Scenario 1:  $w_0 = 0.01$ ; Scenario 2:  $m_0 = 0.035$ ;  
 847 Scenario 3:  $\varphi_0 = 0.0037$ ; Scenario 4:  $\varphi_0 = 0.0018$ ,  $R = 10$ ; Scenario 5:  $\delta_0 = 0.0014$ , in Scenario 6  
 848  $M_0 = 0.02$ ,  $Q = 20.9$ .

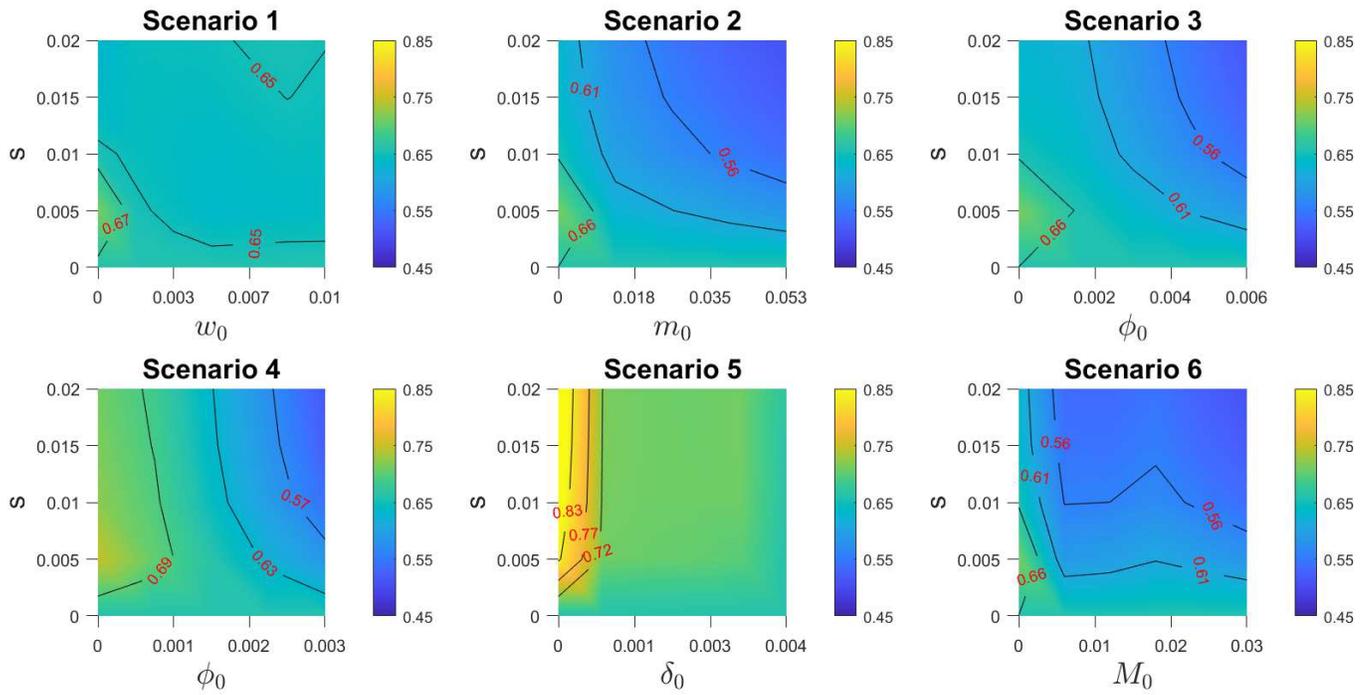
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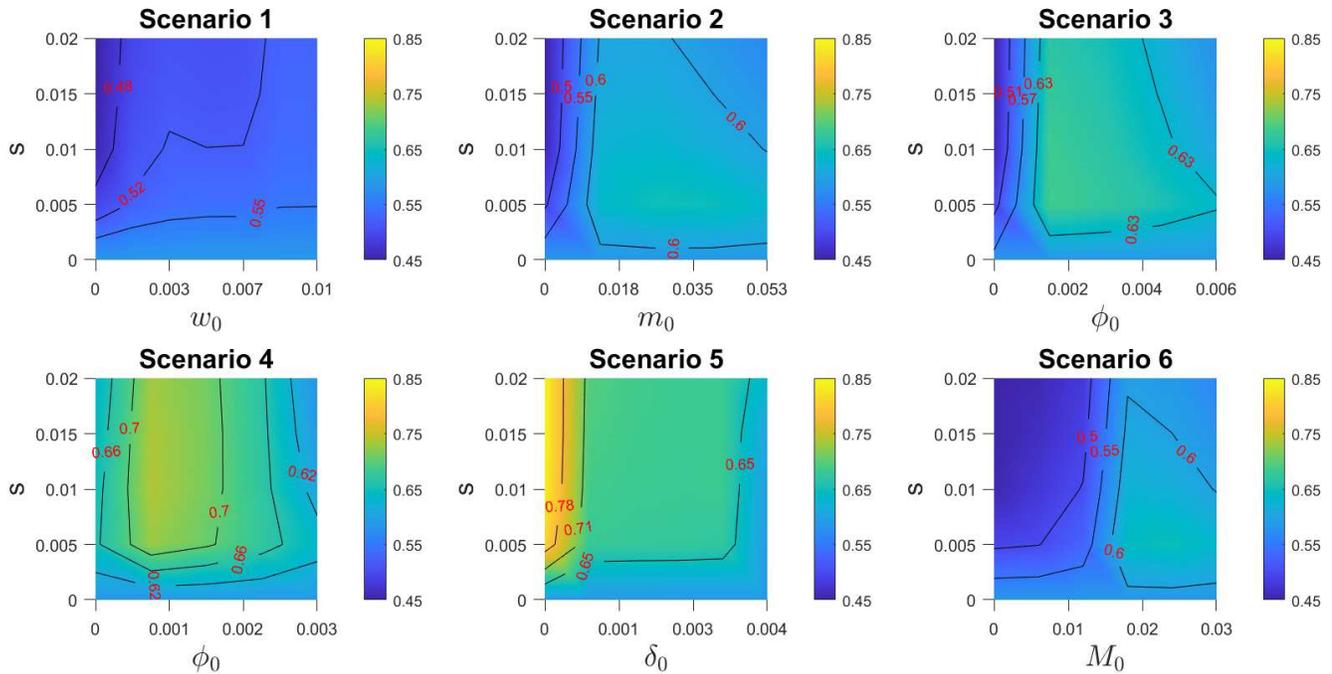
851 Supplemental Figure C. Locations and times when the home ranging component of the  
 852 consumer population is actively switching into the diffusive foraging model for cases with two  
 853 in-phase resource patches. Note that the blue and yellow portions of the plots are largely  
 854 complementary to those in Fig. 2. However, in scenario 5 (panel e), the switching to diffusion  
 855 takes place as the resource peak is waning not increasing. Fixed parameters:  $\theta = 0.01$ ,  $D = 0.1$ ;  
 856 Scenario 1:  $w_0 = 0.01$ ; Scenario 2:  $m_0 = 0.035$ ; Scenario 3:  $\varphi_0 = 0.0037$ ; Scenario 4:  $\varphi_0 =$   
 857  $0.0018$ ,  $R = 10$ ; Scenario 5:  $\delta_0 = 0.0014$ ; Scenario 6  $M_0 = 0.02$ ,  $Q = 20.9$ .

858

859 Top:



861 Bottom:

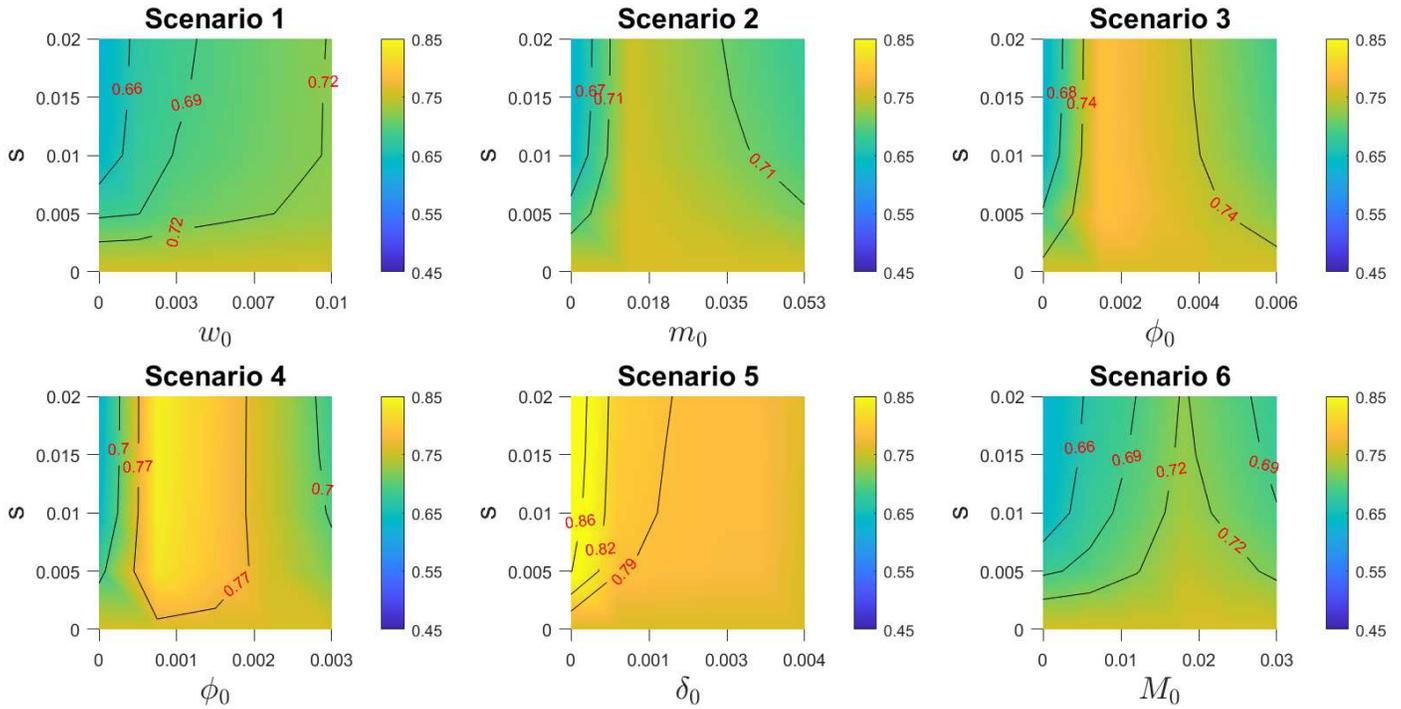


863 Supplementary Figure D. Resource matching with a single resource peak. Fixed parameters:  $D = 0.1$ ,  $\theta =$

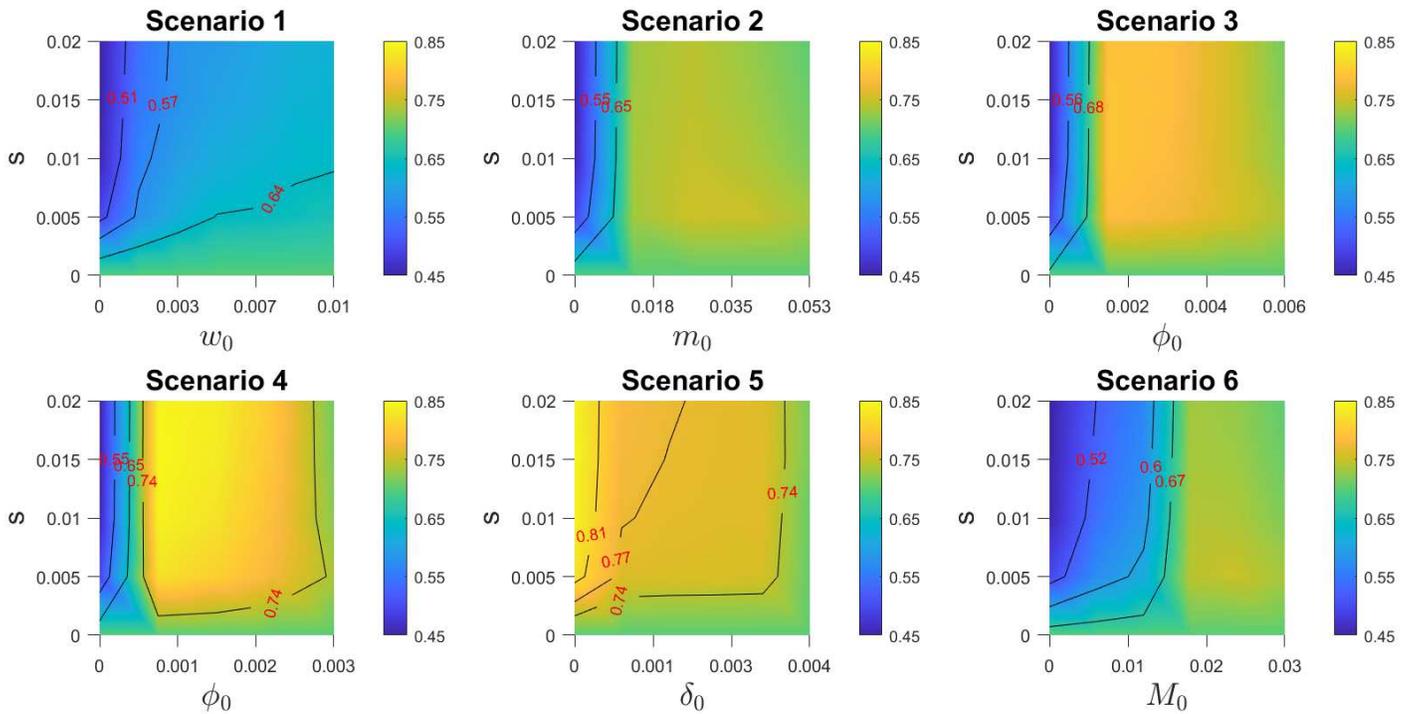
864  $0.005$  (top array),  $\theta = 0.02$  (bottom array).

865

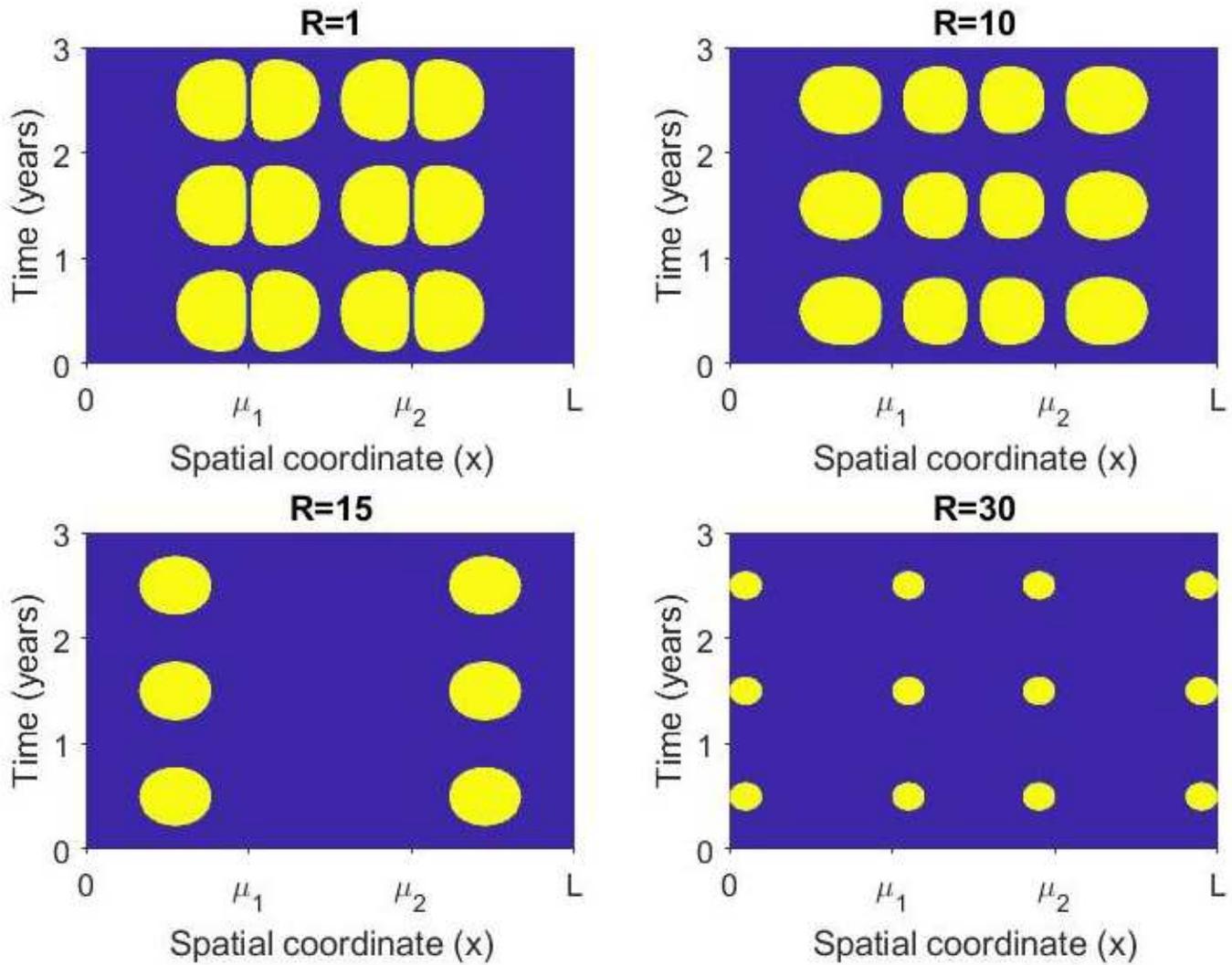
866 Top:



868 Bottom:



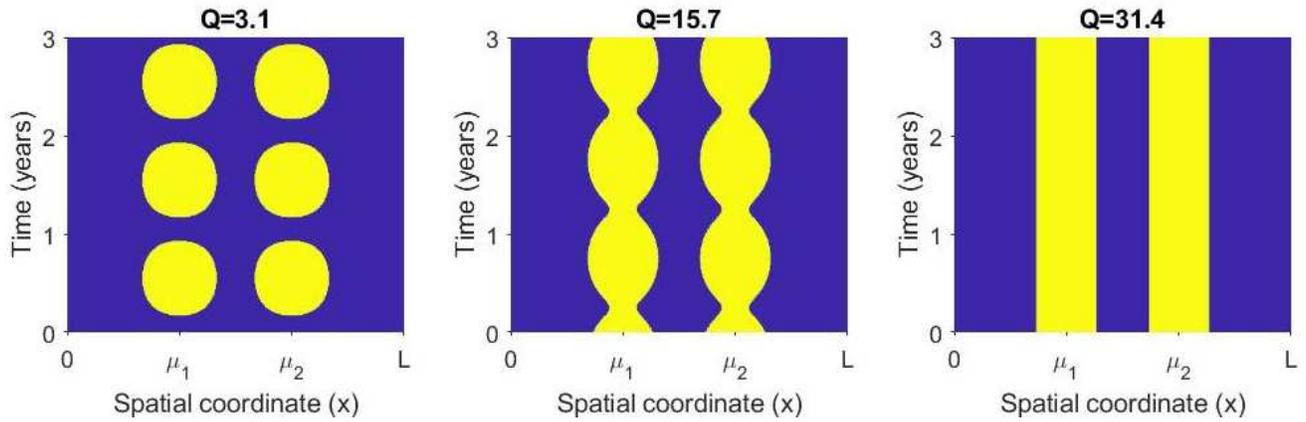
870 Supplementary Figure E. Resource matching with two in-phase resource peaks. Fixed parameters:  $D=0.1$ ,  
 871  $\theta=0.005$  (top array),  $\theta=0.02$  (bottom array).



873 Supplemental Figure F. For the case of two in-phase resource patches, locations and times when  
 874 the resource conditions in Scenario 4 favor the consumer population to actively switch from the  
 875 diffusive foraging mode to the home ranging mode as a function of the perceptual range,  $R$ . To  
 876 be clear, this plot is showing the locations where the switching is actually taking place, not the  
 877 perceptual radii themselves. Thus, based on very large perceptual radii, it turns out that the  
 878 switching should only happen in selected small areas. Yellow:  $\alpha = s$ , Blue:  $\alpha = 0$ . Parameters:  $L$   
 879  $= 100$ ,  $\mu_{\square} = 33.3$ ,  $\mu_{\square} = 66.6$ ,  $\varphi_0 = 0.001$ .

880

881



883 Supplemental Figure G. Portions of space-time when the consumer population in Scenario 6 is  
 884 actively switching from the diffusive foraging mode to the home ranging mode as a function of  
 885 memory length,  $Q$ , for the case of two in-phase resource patches. Yellow:  $\alpha = s$ , Blue:  $\alpha = 0$ .  
 886 Parameters:  $L = 100$ ,  $\mu_1 = 33.3$ ,  $\mu_2 = 66.6$ ,  $M_0 = 0.01$ .

887