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25 organization (sections) of the work.

26 **Abstract**

27 Understanding the structural complexity and the main drivers of animal
28 search behaviour is pivotal to foraging ecology. Yet, the role of
29 uncertainty as a generative mechanism of movement patterns is poorly
30 understood. Novel insights from search theory suggest that organisms
31 should collect and assess new information from the environment by pro-
32 ducing complex exploratory strategies. Based on an extension of the first
33 passage time theory, and using simple equations and simulations, we unveil
34 the elementary heuristics behind search behaviour. In particular, we show
35 that normal diffusion is not enough for determining optimal exploratory
36 behaviour but anomalous diffusion is required. Searching organisms go
37 through two critical sequential phases (approach and detection) and expe-
38 rience fundamental search tradeoffs that may limit their encounter rates.
39 Using experimental data, we show that biological search includes elements
40 not fully considered in contemporary physical search theory. In particu-
41 lar, the need to consider search movement as a non-stationary process
42 that brings the organism from one informational state to another. For
43 example, the transition from staying in to leaving out an area may occur
44 through an exploratory state where cognitive search is challenged. There-
45 fore, a more comprehensive view of foraging ecology requires including
46 current perspectives about movement under uncertainty.

47 **Keywords:** search behaviour, foraging ecology, animal movement, ran-
48 dom walks, Lévy walks, composite correlated random walks.

49 1 Search behaviour and foraging ecology

50 The current paradigm of foraging behaviour assumes that animal movement is
51 mostly informed and that motor control is essentially reactive to environmental
52 cues (Turchin, 1998; Dusenbery, 1992; Stephens, 2007). For example, movement
53 within resource patches is mostly guided by sensory information (e.g. taxis,
54 kinesis), whereas movement between patches is assumed to be driven by memory
55 or large-scale navigation (Turchin, 1998; Schick *et al.*, 2008; Benhamou, 2014).
56 Nevertheless, movement behaviour should also respond to active sampling of
57 the environment, typically when information is lacking and patches need to be
58 found or when some information exists but biological constraints associated to
59 perception or learning pervade (Bell, 1991; Lima & Zollner, 1996; Stephens,
60 2007; Lihoreau *et al.*, 2012; Higginson & Ruxton, 2015).

61 Organisms can incorporate, store, and use relevant information to form in-
62 ternal models about the outside world (McNamara, 1982; Olsson & Brown,
63 2006; Pearce-Duvet *et al.*, 2011). These internal models may serve to dynam-
64 ically couple expectations with planned movement. In this sense, *sampling*
65 *behaviour* is connected with information processing. Concordantly, a Bayesian
66 forager (Oaten, 1977; Krakauer & Rodriguez-Gironés, 1995; Olsson & Brown,
67 2006; McNamara *et al.*, 2006; van Gils, 2010), always has a prior expectation
68 about some aspect of the environment, for example, it may have had a recent
69 successful encounter or an expectation of the availability of resources. Bayesian
70 updating and entropy maximization have been suggested as the fundamental
71 building mechanisms of such internal models (Calhoun *et al.*, 2014; Hein &
72 McKinley, 2012; Hills *et al.*, 2015); however, it is not yet clear how animals
73 acquire and dynamically maintain or adjust such prior expectations (Olsson &
74 Brown, 2006; McNamara *et al.*, 2006). How reliable or robust are such pri-
75 ors? How do animals change their mind about priors? Can search behaviour
76 reduce the negative effects of environmental noise, error perpetuation, or the
77 acquisition of biased expectations (Lihoreau *et al.*, 2012; Hills *et al.*, 2015)?

78 Foraging animals experience different “informational contexts” that lead to
79 different motivational states and motor output (Morales *et al.*, 2010). Active
80 search behaviour (i.e. strategic sampling) is one such motivational state. More
81 broadly, from a behavioural perspective, it is important to understand how
82 animals transition back and forth from informed to relatively uninformed be-
83 havioural states. In other words, how do animals prioritize and use prior infor-
84 mation when searching, so it can capitalize on either exploitative or exploratory
85 movement strategies, respectively (Vergassola *et al.*, 2007; Hein & McKinley,
86 2012). As suggested in McNamara *et al.* (2006) the optimal weight would de-
87 pend on the specificity of the prior information and the quality of the current
88 observations. However, from an evolutionary perspective, it is important to
89 acknowledge that distinct selection pressures on search movement traits exist
90 and depend on the informational context. Animals may adapt their search
91 behaviour differently depending on whether the need is to unfold explorative
92 strategies (e.g. fundamental information gathering, low information availability)
93 or exploitative strategies (e.g. chemotaxis, area restricted search, or purposeful
94 relocation movements to abandon a given area).

95 **1.1 Search tradeoffs and information use**

96 One might assert that there is a clear contradiction between the idea of *random*
97 search (as probabilistic, uninformed movement) and the fact that organisms
98 have evolved sensory and cognitive skills to exploit the environment. Never-
99 theless, biological details make this contradiction less apparent. Sensory and
100 cognitive capacities are limited and thus any organism face situations of un-
101 certainty when foraging. Random search theory can help us understanding the
102 fundamental tradeoffs in these low-information situations and to identify the
103 rules that lead to successful sampling.

104 In a random search process, three main elements govern encounter success:
105 (i) speed, (ii) turning patterns, and (iii) perception (Méndez *et al.*, 2014a). Here,
106 we hypothesize that the combination of speed, turning and perception define two

107 key compromises of random search (Figure 1): (i) the *speed-perception* tradeoff
108 where high speeds improve the spreading capacity but reduce perceptual capa-
109 bilities (Dusenbery, 1992; Campos *et al.*, 2013), and (ii) the *intensive-extensive*
110 tradeoff, which is the fundamental compromise between being able to encounter
111 nearby targets (intensive search mode) and at the same time find faraway tar-
112 gets (extensive search mode), in areas that might be more profitable (Raposo
113 *et al.*, 2011; Bartumeus *et al.*, 2013, 2014; Méndez *et al.*, 2014b).

114 Both, the speed-perception and the intensive-extensive tradeoff define a bi-
115 dimensional space where limiting cases can be identified (Figure 1). In realistic
116 biological scenarios, the two tradeoffs are not independent because they both
117 depend on the organisms' speed: as speed increases, both perception and turn-
118 ing decrease. Therefore, for the case of biological searches, only a subset of the
119 potential space depicted in Figure 1 is accessible. In such a domain different
120 informational contexts may coexist (represented as an information-availability
121 landscape in Figure 1). Indeed, the combination of two fundamental tradeoffs
122 and the presence of informational gradients is believed to frame any search pro-
123 cess, defining three fundamental search states: exploitation, exploration, and
124 relocation (Figure 1). Two of them (exploitation and relocation) are aligned
125 with informed decision-making, for example, either staying in an area (lead-
126 ing to an area-restricted type of motion) or leaving out the area (leading to
127 straight-lined or ballistic motion). These two states involve two limiting be-
128 haviours represented in the lower-left and the upper-right corners of the search
129 tradeoff space, where maximal information usability is also depicted (Figure 1).
130 Our working hypothesis is based in the principled guess that the transition be-
131 tween the stay-leave decisions (exploitation vs. relocation) often requires a third
132 state (exploration) that leads to complex movement patterns aimed at gathering
133 more information. Many behavioural transitions may exist between stay-leave
134 states (i.e. paths transiting from the lower-left to the upper-right corner in Fig-
135 ure 1), but only paths around the diagonal adequately balance the two tradeoff
136 conditions, unfolding the most effective sampling movement possible. Paths

137 crossing the upper-left and the lower-right corners (Figure 1) involve either too
138 blind or too slow exploratory behaviours, respectively, suggesting suboptimal
139 and less biologically plausible stay-leave transitions.

140 Figure 1 redefines search as a ternary (i.e. exploitation-exploration-relocation)
141 instead of a binary (i.e. exploitation-exploration) process (Hills *et al.*, 2015).
142 Indeed, we suggest that the exploration and the relocation states are erroneously
143 unified and that the understanding of the transition dynamics between the three
144 states identified here is fundamental for the comprehensive inclusion of search
145 behaviour in foraging ecology. In particular some questions are: (i) how are
146 search states associated with movement behavioural modes?, (ii) does the ex-
147 ploration state represent a short or a long transient between the two more in-
148 formed states?, (iii) what are the elementary constraints and optimization rules
149 governing the exploration state?, (iv) which motion patterns emerge during the
150 exploratory state?

151 Guided by these ideas (Figure 1), we place current random search theory into
152 an eco-evolutionary perspective. First, we identify key spatiotemporal scales of
153 the search process that need to be considered to understand the search be-
154 haviour of the organism. Second, we show that not only the total amount of
155 area covered but also how the area is filled (i.e. space use) is crucial to optimize
156 a random search strategy. Third, we evaluate the key role of speed and diffusion
157 in the speed-perception and the intensive-extensive tradeoffs by running simula-
158 tions covering a wide range of the key parameters. Fourth, we analyze empirical
159 trajectories of *C.elegans* in a specific search context, showing why biological de-
160 tails (i.e. information-processing, internal states, and motor constraints) are
161 important for the understanding of search behaviour in the context of forag-
162 ing ecology. Finally, we suggest further experiments to explore the usefulness
163 and validity of the proposed new search paradigm in general foraging-ecology
164 research.

165 2 Factoring the time to find a target

166 Different measures can be employed to calculate search efficiency (e.g. Preston
167 *et al.*, 2010; Chupeau *et al.*, 2015; Kagan & Ben-Gal, 2015; Campos *et al.*,
168 2015a), and their suitability basically depends on the target density (resource
169 concentration in a foraging context). Encounter rates, for instance, are useful
170 measures of efficiency for high target densities in which time between consec-
171 utive encounters is small compared to other relevant biological scales such as
172 the directional persistence and foraging trip duration (Berg & Purcell, 1977;
173 Gerritsen & Strickler, 1977; Dusenbery, 1992; Kiorboe, 2008). Situations with
174 low target densities (i.e. relatively long times between encounters) are typi-
175 cally described through the Mean First Passage Time (MFPT) (Redner, 2001;
176 Shlesinger, 2007; Méndez *et al.*, 2014a), defined as the average time $\langle T \rangle$ for
177 the searcher to hit a target, given some initial condition. The latter is a more
178 appropriate measure to account for the dynamics of *exploratory* strategies as
179 those described in Figure 2, in which successful encounters are well separated in
180 time because they occur only after a large number of movement events. How-
181 ever, by definition the MFPT assumes perfect detection and thus captures only
182 the statistics of *first-passages*. Consequently, this measure cannot address the
183 aforementioned speed-perception tradeoff, since it does not consider the possi-
184 bility that a target may be missed and that multiple *passages* may occur before
185 detection (Bartumeus & Levin, 2008; Reynolds & Bartumeus, 2009). For this
186 reason a more general concept, the Mean-First Detection Time (MFDT) has
187 been formally introduced in recent works (Campos *et al.*, 2012, 2013) and will
188 be considered here.

189 To calculate MFDTs one must consider (see also Box 1), (i) the movement
190 parameters: speed v , angular correlation α , and “flight time” distributions $\varphi(t)$,
191 where t represents jump or displacement durations. These parameters ulti-
192 mately define a diffusion constant $D(v, \alpha, \varphi(t))$, (ii) detection parameters: a
193 probability of detection as a function of speed $p(v)$, and (iii) boundary con-

194 ditions: a typical domain size (characterized by the average mean free path
 195 between targets L), which also determines the density of targets, a generic per-
 196 ceptual scale defined here as the sum of the searcher perceptual scale and the
 197 target size $R = r_s + r_t$, where $R \ll L$, and an initial distance x_0 of the searcher
 198 to the closest target, which represents the minimal distance required to leave
 199 the empty area within the search domain.

200 The expression for the MFDT in statistical mechanics in the context of
 201 search can be generalized as (Campos *et al.*, 2013):

$$\langle T \rangle = T_1 + T_2 \quad (1)$$

202 where $T_1 = f_1(x_0, D, L, R)$ and $T_2 = f_2(v, p(v), L, R)$. In this way, the search
 203 process is divided into two temporal phases: (1) the mean time needed to leave
 204 the empty area defined by the distance to the closest target, during which the
 205 probability of detecting a target is zero or negligible on average, i.e. T_1 , and
 206 (2) the mean time needed to detect a target, once the searcher probability of
 207 detection is non-negligible on average, i.e. T_2 .

208 During the approaching phase (i.e. T_1), the average detection is zero and the
 209 distance from the initial position to the closest target x_0 , and the type of dif-
 210 fusive process D are the limiting factors determining the probability to reach a
 211 target. The probability to detect targets in the T_2 phase, depends mostly on the
 212 speed v and the perception ability as a function of speed $p(v)$. Motion in T_2 may
 213 include subsequent back-and-forth movements away and towards the targets so
 214 it might appear puzzling that T_2 does not depend explicitly on D . The explana-
 215 tion for this is that when directional persistence has a single (or predominant)
 216 characteristic scale it plays an ambivalent role that neutralizes the effects of the
 217 diffusion coefficient D in the term T_2 . Whenever the searcher moves towards
 218 the target, an increase in directional persistence (or characteristic flight time)
 219 facilitates encounters with targets. However, if it is in the wrong direction, the
 220 same increase may impair encounters with relatively close targets. The general

221 result is that whenever D is governed by one single characteristic flight time
222 the effect of D on T_2 is cancelled out (for further details see the Supporting
223 Information). Nonetheless, the introduction of multiple persistence scales (or
224 flight times), either due to the effect of heavy tails or multimodal distributions
225 solves this limitation and introduces the possibility of further search optimiza-
226 tion (Bartumeus *et al.*, 2014; Campos *et al.*, 2015b). Other mechanisms not
227 explored here can also lead to non-monotonic effects of directional persistence
228 in first-passage times (Tejedor *et al.*, 2012).

229 Motion (i.e. diffusion) and detection capabilities operate simultaneously
230 throughout the search process. The two processes cannot be readily factorized
231 when considering a single trajectory. Instead, the factorization emerges at a
232 statistical level. T_1 and T_2 are *average* times corresponding to the statistical
233 expectation for a single searcher to find a target at a given time (MFDT).
234 Such statistical expectation is generated by an ensemble of trajectories that
235 represent the set of potential trajectories unfold by an individual searcher. The
236 factorization in Eq. 1 highlights the fact that this expectation is built from two
237 distinct components. A first component in which the searcher needs to cover
238 a distance (x_0) or area such that whatever the path taken the probability to
239 detect a target is necessarily zero (i.e., it is impossible for the searcher reaching
240 any target within T_1). A second component that starts from a set of potential
241 positions achieved at the end of T_1 , such that whatever the path taken from
242 there onwards there will always be a finite probability to detect a target. In
243 other words, once the search starts and a minimal distance or area is covered
244 (i.e. T_1), the potential set of unfolded trajectories have spread out sufficiently
245 for the T_2 period to be initiated (Figure 2).

246 If one extends the random search problem to systems with an arbitrary
247 number of dimensions d , the computation of the MFDT needs an additional
248 characteristic scale, the target size (also interpreted as an effective detection
249 distance in Méndez *et al.* (2014a)). This is essentially defined as the charac-
250 teristic distance between the target and the searcher so that on average target

251 detection becomes significant. Note that in one-dimensional systems the target
 252 can be considered as a point (zero effective size) since the random walker will
 253 pass sooner or later through that point with probability 1. The latter is not true
 254 in higher dimensional systems. For a random walk with persistence modelled
 255 as a Correlated Random-Walk (CRW) starting at an arbitrary position x_0 of
 256 a d -dimensional spatial domain with a mean-free path between targets L , the
 257 equation for the MFDT can be written as (Campos *et al.*, 2013):

$$\langle T \rangle = \frac{\overbrace{L^2}^{T_1} g_d(x_0/L)}{2D} + \frac{\overbrace{L^d}^{T_2}}{R^d \langle vp(v) \rangle} \quad (2)$$

258 Here, $g_d(x_0/L)$ is a function, which implements the effect of the initial condi-
 259 tions, and R^d presents the *effective detection surface/volume* of the target; in
 260 two dimensions this can correspond either to the actual area of the target or
 261 its cross section, depending on the ratio between the characteristic scales in the
 262 problem (see Campos *et al.* (2013) for further details). This function's exact
 263 form depends on the specific dimension of the system. The one-dimensional
 264 case leads to the simple expression (Campos *et al.*, 2012):

$$\langle T \rangle = \frac{\overbrace{L^2(x_0/L)(1-x_0/L)}^{T_1}}{2D} + \frac{\overbrace{L}^{T_2}}{Rvp(v)} \quad (3)$$

265 Note that both Eq. 3 and Eq. 2 preserve the scaling and interpretation
 266 made in Figure 2 for T_1 and T_2 , such that (i) the size of the target, which is
 267 essentially related to the detection probability, only appears in T_2 but not in
 268 the approaching time T_1 , (ii) the diffusion coefficient D is present in T_1 but not
 269 in T_2 (see Supporting Information for further insights), and (iii) the time T_1
 270 always fulfils the diffusive scaling $\sim L^2$ while the detection time T_2 scales as L^d ,
 271 since the time to detect the target in a stationary situation is proportional to
 272 the empty volume of the system (or target density).

273 In accordance to our discussion above, the first term T_1 captures through
 274 the diffusion constant D the effect on the MFDT of both the speed and the

275 turning behaviour, which determines to a great extent the intensive-extensive
276 tradeoff. The second term includes the speed-perception tradeoff in the form
277 $vp(v)$, which can be interpreted as a perception-weighted speed. We note that
278 for the case of particles with perfect detection abilities (i.e. $p(v) = 1$, so the
279 MFDT reduces to the MFPT), Eq. 3 simplifies to the classical result for CRWs
280 derived by George Weiss three decades ago (Weiss, 1984). The relative weight of
281 T_1 and T_2 (and the associated tradeoffs) on $\langle T \rangle$ depends on whether targets are
282 near ($T_1 \leq T_2$) or distant ($T_1 \gg T_2$). In addition, the optimal modulation of the
283 intensive-extensive tradeoff through changes in speed and reorientation patterns
284 also depends on whether targets are nearby or faraway. If targets are both
285 nearby and faraway, the optimal diffusivity (speed and turning patterns) must
286 balance out the probability of leaving a nearby target (to look for a new one)
287 with the probability of staying near the undetected target (Raposo *et al.*, 2011;
288 Bartumeus *et al.*, 2014; Méndez *et al.*, 2014b). If targets tend to be faraway, the
289 general solution is to maximize the probability of leaving the current position
290 in order to approach new targets. If targets tend to be nearby then the solution
291 is to remain close by and meander around until detection.

292 These simple models (Eqs. 3 and 2) emphasize that in a search process,
293 the spacing and distribution of resources are relative to searcher position and
294 perceptual scales (i.e. x_0/L , R) and matter to the extent they modify the
295 searcher encounter statistics (average and variation of the encounter time inter-
296 vals). Nonetheless, an organism-centred view of the resource spacing is notori-
297 ously difficult to capture in a single meaningful metric (Lima & Zollner, 1996).
298 The key temporal and spatial scales identified in the search model are linked to
299 the organisms perceptual scales in a complex way. The connection is not only
300 dependent on the densities and distribution of resources and consumers, but
301 also on cue-related spatial gradients, physical topography, forager motivation,
302 history of experience or age, and social processes. Clearly, the framework pre-
303 sented here is limited in the sense of compacting all these relevant aspects into
304 one single metric, the searcher-to-target nearest distances.

305 **3 Diffusion and space use**

306 In principle, it may seem that the ultimate goal of search is to explore more
307 territory in less time. However, search efficiency measures success in finding
308 targets, not in covering space; therefore, despite the fact that the maximization
309 of space coverage is important, and in many occasions correlates positively with
310 search efficiency, it is not always the best strategy. If near and faraway targets
311 are to be found, then the intensive-extensive tradeoff emerges, and one finds
312 that the search efficiency does not depend strictly on the amount of territory
313 explored per unit time (i.e. D) but on *how* this territory is explored to find
314 the target. In particular, persistent motion alone is not enough to efficiently
315 optimize both close and distant target encounters (Bartumeus *et al.*, 2005).

316 The impact of the diffusion coefficient D on search efficiency through the bal-
317 ance of the intensive-extensive tradeoff, can be clearly shown by Monte Carlo
318 simulations in one-dimensional systems. In Figure 3, we show how the search ef-
319 ficiency, measured as a MFPT (perfect detection), varies as we change diffusion
320 for different flight time distributions (i.e. $\varphi(t)$), and for the two limiting search
321 regimes, asymmetric (the nearest targets can be either very close or far away
322 from the searcher) and symmetric (the nearest targets are at a similar distance
323 from the searcher). Whether a landscape is homogeneous or heterogeneous is a
324 property defined by the spatial distribution of the targets, whereas the notion
325 of asymmetric/symmetric search regimes is featured by the starting position of
326 the searchers, hence, a local property. In principle, homogeneously distributed
327 target fields promote symmetric search regimes, whereas patchy or heteroge-
328 neously distributed targets promote asymmetric search regimes. However, it
329 must be noted that the average relationship between local and global landscape
330 properties take a time to converge, the convergence rate depending on both the
331 landscape structure and the searcher movement. Hence, in a search process, the
332 amount of patchiness and the amount of local variation in the nearest searcher-
333 to-target distances are expected to be correlated but are not exactly the same

334 thing.

335 In our example (Figure 3), the increase in D along the x -axis is achieved
336 by keeping the velocity constant and only changing the parameters that af-
337 fect the flight time distribution. Note that for a given spreading capacity
338 (i.e. D) the MFPT changes depending on whether the microscopic movement
339 leads to normal or anomalous diffusion (Seuront & Stanley, 2014; Benhamou,
340 2014; Bartumeus, 2015). Different mechanisms leading to anomalous superdif-
341 fusion have been suggested, either through enhanced (D_{enh}) or composite dif-
342 fusion (D_{comp}) (Bartumeus *et al.*, 2005; Benhamou, 2007; Raposo *et al.*, 2011;
343 Reynolds, 2012; Bartumeus *et al.*, 2014) (see also Box 1). Importantly, both
344 types of non-Brownian diffusivity decrease the MFPT (i.e. T_1 of Eq. 1) at inter-
345 mediate D 's. Also, the search efficiency improves compared to a simple diffusive
346 process, driven by an exponential distribution of flight times (Eq. 5) and also
347 to straight-lined motion. Both D_{enh} and D_{comp} may result in a similar search
348 efficiency and may be better than D_{corr} , where single-scaled persistence or char-
349 acteristic flight times is incorporated. Hence, Figure 3 confirms that the optimal
350 balance between intensive-extensive search cannot be unequivocally determined
351 by D but depends on the microscopic details of the turning patterns, in par-
352 ticular the inter-turn time or flight time distribution $\varphi(t)$. Turning patterns
353 balance out the capacity of the searcher to move away and come back from/to
354 the target. Such a balance requires multi-scaled (and far from Gaussian) move-
355 ment patterns (Bartumeus *et al.*, 2014; Méndez *et al.*, 2014b). The latter can
356 be achieved either by generating a mixture of D 's with different Gaussian pa-
357 rameters for speed and flight times (D_{comp}), or by incorporating heavy-tailed
358 speed and flight time distributions (with a slower decay than Gaussian but fi-
359 nite moments) within one single D (D_{enh}). Currently, defining the generative
360 mechanisms leading to anomalous dynamics (departures from normal diffusion)
361 is an active field of research (Benhamou, 2007; Heisenberg, 2009; Brembs, 2011;
362 Bazazi *et al.*, 2012; Campos *et al.*, 2014; Salvador *et al.*, 2014; de Jager *et al.*,
363 2014; Wearmouth *et al.*, 2014; Reynolds, 2015).

364 In the Supporting Information, we show the derivation of D_{comp} and D_{enh} ,
365 and its relationship with flight time distributions. We also show how velocity
366 (i.e. speed) alone may modulate the capacity to detect nearby targets, modifying
367 the optimal values of the speed-perception tradeoff. A summary of the main
368 results is found in Box 1.

369 4 Search optimization

370 While the discussion in the previous section illustrates the crucial scales and
371 tradeoffs influencing search processes, they may give the false impression that
372 the two fundamental search tradeoffs (i.e. intensive-extensive, speed-perception)
373 can be optimized independently. This is not true since both perception and the
374 diffusion constant D are affected by the searcher speed. Hence, a unique global
375 optimum that minimizes the search time can be determined, but requires a com-
376 plete parameterization of the problem that includes search behaviour (movement
377 and perception) and the landscape properties.

378 Here we perform a comprehensive, quantitative analysis. The searcher moves
379 within a domain which is large enough so boundary effects are negligible (large L
380 with periodic boundary conditions), and fights are at constant speed separated
381 by turning events (uniformly random direction). Target density is represented
382 by $1/L^d$, where d is the spatial dimension. We analyzed two qualitatively dif-
383 ferent search regimes. In the symmetric regime, the searcher starts moving
384 from any point in the whole domain drawn from a uniform distribution. This
385 scenario reflects an average distance towards the closest target of the order of
386 the domain size, representing an homogeneous landscape from the perspective
387 of the searcher. In the asymmetric regime, the searcher starts from any point
388 drawn from a Gaussian distribution with variance $\sigma = 2R^2$ centred at a given
389 target position, where $R = r_t + r_s$ is the sum of the detection scales or radius
390 of the target r_t and the searcher r_s . As $R \ll L$ the typical scales of the dis-
391 tance to the close-by ($2R^2$) and faraway (L) targets are different, representing

392 a heterogeneous landscape from the searcher perspective.

393 The whole spectrum of possible search strategies depicted in Figure 1 has
394 to be explored in order to look for global optimal compromises based on these
395 tradeoffs. We characterized the intensive-extensive tradeoff through the diffu-
396 sion coefficient D , computed from the microscopic parameters (see Box 1), and
397 the speed-perception tradeoff using the speed v along with the speed-dependent
398 factor $e^{-\gamma v}$, which determines the probability of detecting the target after pass-
399 ing over it ($\gamma > 0$). In these simulations we consider that perception occurs
400 once per flight, instead of considering a continuous process. While alternative
401 choices of parameters would be possible, the choice of D and v is appropriate as
402 it encompasses the whole decision-making set of possibilities that the searcher
403 has available to improve its strategy. Figure 4 compares the MFDT obtained
404 as a function of the diffusion coefficient (i.e. varying $\varphi(t)$ and keeping speed
405 as a constant), and speed for: (i) exponential and truncated-Lévy flight time
406 distributions (a paradigmatic heavy tail distribution, common in empirical ob-
407 servations, and easy to handle when computing the effect of heavy-tailed flight
408 times), and (ii) different detection parameter values $\gamma = 0, 0.1, 0.2, 0.5$ (in or-
409 der to determine the effect of perceptual capabilities, the larger the detection
410 parameter γ the smaller the probability of detection), and (iii) two types of
411 initial conditions, leading to two different search regimes (Raposo *et al.*, 2011;
412 Bartumeus *et al.*, 2013, 2014). In our simulations we are not considering any
413 energetic cost related to speed (e.g. speed as a function of energy cost or speed
414 limits) which could have additional effects on search efficiency beyond the effects
415 of the speed-perception tradeoff explored here.

416 For the exponential flight time distribution (Figure 4, upper panel) and
417 for *easy detection* conditions ($\gamma = 0, 0.1$), the global optimum strategy (low
418 MFDTs) lies in the region of a large diffusion constant (D) and high speed (v).
419 The result is qualitatively similar for both search regimes (symmetric or asym-
420 metric). Concordantly with Reynolds & Bartumeus (2009), as perception error
421 increases and target detection becomes less probable the global optimum is dis-

422 placed towards smaller values of speed (the slow, scanning limit) and smaller
423 values of D (intensive search limit) compared to the case with perfect detec-
424 tion. Noticeably, the confinement of the optimal solution (low MFDT values) at
425 small values of D is stronger in the asymmetric than in the symmetric regime.
426 So, searchers strongly constrained by perception will benefit from using mod-
427 erate speeds and intensive strategies in order to revisit places several times to
428 balance possible detection failures. This solution is more relevant when nearby
429 targets exist, and importantly, we have checked numerically that this tendency
430 is independent of the details of the detection process (e.g. using other func-
431 tions $p(v)$ or introducing more complicated movement patterns which include
432 pauses). So the necessity for slowing down and enhancing revisits (intensive
433 search) when perception is impaired seems to be a rather general and robust
434 conclusion and may only depend quantitatively from certain details on how the
435 perception process is implemented.

436 For the truncated Lévy flight distribution (Figure 4, lower panel) the most
437 conspicuous effect on the global optima is the shift from high to low speed, as the
438 probability of detection decreases (i.e. γ increases). Note that when detection
439 is close to perfect ($\gamma = 0, 0.1$), the negative impact of small D values on search
440 efficiency is much less important in the Lévy than in the exponential case.
441 This is because the truncated Lévy distribution can generate a non-negligible
442 proportion of large ballistic displacements (due to the heavy-tail) that allows
443 for improved search efficiency (low MFDT) even at low D values. Also different
444 from the exponential case is that when detection probability becomes small ($\gamma =$
445 $0.2, 0.5$) large diffusion values are still able to produce low MFDT values. This is
446 because large diffusion coefficients based on heavy-tailed microscopic movement
447 can still hold an adequate balance between intensive and extensive search modes.
448 The right balance should allow for revisiting areas with a frequency that is short
449 enough to decrease detection failures but large enough to avoid oversampling.

450 **5 Search beyond physics: an experiment with** 451 **nematodes**

452 Discerning among potentially different search states and characterising specific
453 movement modes associated to them (Figure 1) is a challenging task. Often,
454 it results controversial whether organisms perform active sampling or they are
455 merely reacting to local environmental cues. Nonetheless, by displacing an
456 organism from a rich- to a poor-resource environment, so that both the quan-
457 tity and the quality of available information changes abruptly, one can inves-
458 tigate how organisms adjust their search behaviour to low information condi-
459 tions (Bazazi *et al.*, 2012; Salvador *et al.*, 2014; Seuront & Stanley, 2014). In
460 resource-rich environments, organisms are well-fed and surrounded by resources
461 but when displaced to a resource-poor and cue-less environment animals start
462 to experience a radically different situation. In such cases, one would expect
463 organisms to *actively* try to gather information near their initial position before
464 deciding to leave. A crucial aspect is whether the transition between exploita-
465 tion (i.e. staying in an area) and relocation (i.e. leaving the area) is determined
466 by exploratory movements, governed by the fundamental tradeoffs and the op-
467 timization mechanisms explained in the above Sections, or alternatively, it is a
468 fast transition governed by relatively informed movement. To address this ques-
469 tion we performed this type of experiment with the nematode *Caenorhabditis*
470 *elegans*.

471 We placed one at a time, 39 *C.elegans* individuals (well-fed on a bacteria
472 lawn for several days) onto a bare agar plate (zero food) of 24.5×24.5 cm at a ho-
473 mogeneous temperature of 21°C , and tracked their movement at high-resolution
474 (32 Hz) for about 90 minutes. In this experimental setup the environment of
475 the worm was carefully controlled, so its movements are mainly determined by
476 the animal's internal state (e.g. starvation level or memory of the previous
477 conditions) and not to any environmental cues (e.g. temperature or chemical
478 gradients).

479 5.1 Search is a non-stationary behavioural process

480 Our working hypothesis is that foraging organisms are confronted with different
481 motivational states and information-availability contexts that modulate move-
482 ment behaviour (Figure 1). Despite our dataset covers a wide range of scales,
483 one must always be cautious when inferring motivational states and true be-
484 havioural processes from movement data.

485 We characterize *C.elegans* movement on the basis of 3 variables including:
486 straightness index (S), net displacement D (or effective velocity, V), and mean
487 travel velocity (T) (see Supporting Information). We use t-Stochastic Neigh-
488 bouring Embedding (t-SNE) (Berman *et al.*, 2014) and classic Hidden Markov
489 Modelling to segment these trajectories into different movement modes (see
490 Supporting Information). Our analysis reveals a complex behavioural land-
491 scape delimited by three statistically significant domains or regions (Figure 5a).
492 Each domain is characterized by a dominant (and differentiated) movement
493 mode among a hierarchical set. The emergence of three large domains in the
494 behavioural landscape suggests the presence of three motivational search states,
495 namely, exploitation, exploration and relocation, which in turn, are character-
496 ized by three dominant movement modes: area-restricted search, sampling, and
497 ballistic-like motion, respectively (Figure 5a). Based on these empirical results
498 we hypothesize that search behaviour is governed by three motivational states
499 that modulate the propensity by the organism of being in one or another move-
500 ment mode. To interpret better the behavioural landscape (i.e., the main do-
501 mains and movement modes) we depict the values of each of the input variables
502 (see Supporting Information) on the landscape (Figure 5b,c,d). In particular
503 S and V can be considered rough surrogates of the intensive-extensive and the
504 speed-perception tradeoffs. Its marked gradation (Figure 5b and c) ensures that
505 the three dominant movement modes represent different tradeoff compromises.
506 Compared to S and V , the mean travel velocity T is more heterogeneously
507 distributed across the landscape. The smallest T 's are strongly associated to
508 area-restricted search behaviour, but small and large T 's can locally co-occur

509 elsewhere in the behavioural landscape.

510 Finally, we use the results obtained from the t-SNE segmentation procedure
511 to feed a 3-state Markov-chain to model the transitions and the overall tempo-
512 ral dynamics of the three search states. We find that the exploitation and the
513 relocation states do never occur consecutively in time but they are rather linked
514 through a differentiated exploratory state (Figure 6b). In addition, the state's
515 prevalence dynamics shows a gradual shift from exploitation to relocation, with
516 an intermediate phase (around minute 70 of the experiment) governed by ex-
517 ploration (Figure 6c). These results are also confirmed when directly modelling
518 the data with 3-state Hidden Markov Models (see Supporting Information).

519 As in Salvador *et al.* (2014), in this experiment the memory of the previ-
520 ous environment (culture plentiful of bacteria) seem to anchor the animal for
521 about 30 minutes around its initial position. Therefore, in this case, the area-
522 restricted search (ARS) is not directly driven by chemotaxis. The exploitation
523 state must be the result of the memory (*sensu latu*) of past resource availability,
524 which may progressively relax due to cumulative failures in sensing resources.
525 In *C.elegans* ARS is maintained mainly using a special type of turn known as
526 pirouettes (Pierce-Shimomura *et al.*, 1999; Ohkubo *et al.*, 2010; Salvador *et al.*,
527 2014). Once the resource memory or expectation has dropped, the worm is en-
528 gaged in an exploratory process aimed at effectively expanding the search area.
529 At this stage, it combines pirouettes with straight-lined crawls, and multi-scale
530 looping behaviour, drifting away from the initial area. Finally, after about 30
531 minutes in the exploratory mode, the worm performs sustained straight-line
532 motion, to the extent that its steering control allows it, suggesting an aim to
533 *relocate* or *leave* the area (Figure 6d). All in all, in well-fed *C.elegans* individuals
534 transiting between stay-leave decisions involves switching from ARS to ballistic-
535 like movement modes and can take about one hour (Figure 6c). These type of
536 transitions are species specific, e.g. well-fed locusts changed from intensive to
537 extensive search much more progressively, in the course of 6 hours (Bazazi *et al.*,
538 2012). Ballistic and fast motion is the optimal strategy for an organism moving

539 in a bare arena, when all targets are faraway (Bartumeus *et al.*, 2005, 2014), but
540 organisms need a time and perform specific motion to figure out this situation.

541 If the transition from an exploitation to a relocation state is optimally in-
542 formed, and hence purely reactive, we would expect the movement behavioural
543 switch to occur in a short time and without intermediate states. However, the
544 existence of a transitional state exploring near and far due to uncertainty may
545 prevent against leaving an area too soon, as ballistic motion strongly under-
546 mines the probability to detect nearby targets, or too late, as ARS does not
547 allow extending the range of search to a neighbouring area. Importantly, the
548 behaviour observed in our experiment is largely suboptimal, that is, in a bare
549 arena, ballistic motion would clearly be the best solution. Therefore, the long
550 and complex behavioural response of *C.elegans* must have evolved as a response
551 to fluctuations in their natural environments.

552 The results revealed that *C.elegans* produces complex locomotory patterns
553 that are not directly related to environmental fluctuations or resource den-
554 sity (Avgar *et al.*, 2011; de Jager *et al.*, 2014). Our data confirms the results
555 in Salvador *et al.* (2014) and Calhoun *et al.* (2014): the transition from area-
556 restricted search to ballistic-like motion in *C.elegans* is not fast nor simple but
557 it entails a long and complex transient period. Therefore this search can be
558 described as a non-stationary behavioural process that drives the worm from
559 the decision of staying in the area to the decision of leaving the area, through a
560 relatively long intermediate stage.

561 **5.2 Behavioural details govern search diffusion**

562 Diffusion is a relevant metric to understand biological search capacity (see Sec-
563 tion 3) but often organisms' movement depart from the idealized microscopic de-
564 scriptions of diffusion (Méndez *et al.*, 2014b). In this sense, the search movement
565 of *C.elegans* is not only *non-stationary* but it clearly departs from the simple
566 *run-and-tumble* random-walk model (Stephens *et al.*, 2010). Indeed, *C.elegans*
567 performs many different types of *turns*, each producing different changes in an-

568 gular direction, and its *runs* are not simple straight paths but rather curvilinear
569 trajectories (Izquierdo & Beer, 2015), with a broad distribution of curvatures.

570 In empirical data, diffusive properties are often evaluated by computing
571 the scaling exponent α of the mean square displacement (MSD) over time
572 ($\text{MSD} \approx t^\alpha$), at the population level. In Stephens *et al.* (2010); Salvador *et al.*
573 (2014), for example, it is shown that *C.elegans* movement departs from normal
574 diffusion for a wide range of scales. Here, we show that the key feature governing
575 the diffusive properties of search is the time-dependent steering control that the
576 worm carries out along the search process (Figure 7 and Supporting Informa-
577 tion). In particular, the three search states previously identified (Figure 5 and
578 Figure 6) can be associated with different diffusivities (Figure 7a) and looping
579 patterns (Figure 7b). The three search states have the same short-ranged MSD
580 (superdiffusive) but for each of them the large-scale curvature of the trajecto-
581 ries shows different characteristic times, reflected in different MSD slopes and
582 large-scale behaviour. The fluctuations observed in the MSD curves (Figure 7b
583 inset) are due to the complex looping behaviour of the worm, clearly departing
584 from standard diffusion and random walk models (Figure 7b inset).

585 The exploitation, exploration, and relocation states clearly reveal distinct
586 space use, based on different looping motifs and diffusivities. At the begin-
587 ning of the experiment, the exploitation phase entails tight loops that slowly
588 drift and overlap each other (Figure 7b, inset). This looping behaviour leads
589 to a strong subdiffusive regime ($\alpha < 1$, see Figure 7a) and to a complex MSD
590 curve that plateaus for a range of scales and then subsequently increases show-
591 ing strong fluctuations at the end (Figure 7b). During exploration, the total
592 area covered is similar to that of the exploitation state but the coverage occurs
593 about four times faster due to marginally superdiffusive behaviour ($\alpha \geq 1$, Fig-
594 ure 7a). In this state, loops are loose and combined with straight-lined segments
595 (Figure 7b, inset). When relocation is taking place the worm generates wide
596 loops (Figure 7b (inset), also called open arcs in Salvador *et al.* (2014)), which
597 generate superdiffusive behaviour ($\alpha > 1$, Figure 7a). In general, the steering

598 control of *C.elegans* cannot avoid systematic orientational biases (Izquierdo &
599 Beer, 2015), impairing ballistic motion in the long-run. In the three states the
600 long-term MSD behaviour converges to (sub)normal diffusion (Figure 7a). A
601 more detailed picture of the MSD behaviour (Figure 7b) reveals that the MSD
602 fluctuations systematically increase through time due to the long-return times
603 to previously visited areas.

604 These results reveal that *C.elegans* shows diffusive variation which cannot
605 be directly associated to environmental fluctuations and resource density (Av-
606 gar *et al.*, 2011; de Jager *et al.*, 2014). In addition, diffusion constants and
607 scaling exponents (MSD slopes) are important and informative parameters, but
608 biological details cannot be forgotten in order to understand search behaviour
609 and efficiency. The study of how sensorimotor constraints and the steering con-
610 trol abilities of *C.elegans* impact on search efficiency through both its effects
611 on diffusion and on small-scale patterns (e.g. looping motifs) needs further
612 investigation.

613 **6 Towards a comprehensive view of foraging**

614 One of the greatest challenges of movement ecology (Nathan, 2008; Schick *et al.*,
615 2008; Smouse *et al.*, 2010; Fronhofer *et al.*, 2013; Benhamou, 2014) is to disen-
616 tangle behavioural processes from movement patterns. Random search theory
617 can provide a background rationale for testing hypotheses about effective for-
618 aging behaviour and help distinguishing active exploration from more informed
619 and reactive types of behaviour in empirical data.

620 Here we have made an explicit connection between classic macroscopic pa-
621 rameters (e.g. diffusion, average speed), mesoscopic movement properties (e.g.
622 directional persistence, flight distributions), target density and distribution (e.g.
623 domain size, symmetric/asymmetric regimes), and search efficiency. We have
624 used both analytical and numerical methods to investigate how movement pro-
625 cesses operating at different scales affect search efficiency. The theoretical results

626 suggest that (i) the organism’s exploratory behaviour may involve two critical
627 temporal phases (i.e. approach and detection), mostly associated with two ba-
628 sic search tradeoffs (i.e. intensive-extensive, speed-perception) and that the (ii)
629 organisms search behaviour should be inherently multi-scaled to balance out the
630 intensive-extensive and the speed-perception tradeoff. Random search theory,
631 however, should be considered just the basic groundwork for understanding bi-
632 ological search phenomena. Other layers need to be added such as the effects
633 of learning, memory, as well as biological details related to motor and cognitive
634 constraints in organisms.

635 We propose to consider foraging behaviour as a three-state, non-stationary
636 process that drive foraging organisms from one state of certainty to another
637 across a bridging state of uncertainty. Foraging uncertainties are about whether
638 to stay (exploit) or to leave (relocate) a given area. Reduced uncertainty can
639 only be achieved through active sampling behaviour, a transient motivational
640 state aimed at gathering information and subject to elementary search trade-
641 offs. Sensory errors and cognitive doubts (i.e. variation in the levels of con-
642 fidence on prior expectations) also justify exploratory states transitioning be-
643 tween relatively more informed states. Ideally, these transients should be brief
644 but Bayesian updating (Olsson & Brown, 2006; van Gils, 2010; Calhoun *et al.*,
645 2014; Hills *et al.*, 2015) is also limited by the computing ability, the motor
646 constraints, and the sampling strategies of the organisms.

647 It has been hypothesized that information processing, modulated by some
648 internal state (hunger, fear, etc), triggers behavioural modes and the transitions
649 among them (Morales *et al.*, 2010). In the most parsimonious (classic) view,
650 foraging involves only two basic motivational states: (i) exploiting the regions
651 with available target information, and (ii) relocating (leaving) to new exploitable
652 areas. However, the combination of these two states can lead to multi-scale
653 (complex) movement behaviour only if the landscape itself or the cues followed
654 by the animal have multi-scale properties (Benhamou, 2007; Schick *et al.*, 2008;
655 Benhamou, 2014). If perfectly informed, such motivational states would gen-

656 erate movement modes closely matching the landscape or its associated cues
657 (Figure 8). Clearly, this classic paradigm is not enough to explain the *grad-*
658 *ual* behavioural transition from exploitation to relocation often observed and
659 sometimes involving complex behaviour. We argue that there is the need to
660 consider at least one more motivational state (and movement mode) between
661 the informed states, which will be related to exploration under uncertainty.

662 In this new paradigm, a richer behavioural repertoire of foraging movements
663 would emerge from the transitions between three rather than two motivational
664 states (Figure 8), corresponding to the exploitation, relocation, and exploration
665 states. In the classic model, positive and negative target cues trigger the ex-
666 ploitation and relocation states, respectively. Here we suggest that ambiguous
667 or unreliable information can trigger active sampling and exploratory behaviour.
668 Following the previous sections such an exploratory state would have evolved
669 to deal with the elementary search tradeoffs, and would have resulted in multi-
670 scale motion patterns that do not necessarily match any landscape feature (Fig-
671 ure 8 and Kölzsch *et al.* (2015)). Figure 8 also illustrates the fact that one
672 could observe multi-scale movement independently of the resource distribution
673 (e.g., multi-scale interpatch motion) and without specifically following landscape
674 cues or memory. In this regard, the question of how exploratory movement be-
675 haviour may help organisms to gather key information about the environment
676 and change prior expectations requires further research.

677 **6.1 Future perspectives**

678 The wide range of theoretical generative mechanisms of search (Reynolds, 2015)
679 makes discovering the true underlying biological mechanisms difficult (Bar-
680 tumeus, 2015). Moreover, the exact biological mechanisms may differ among
681 organism according to their evolutionary history. In our view, the solution to
682 better linking process to pattern in the study of foraging movement, and in par-
683 ticular, understanding how foraging organisms decide whether to capitalize on
684 exploratory or exploitative movement strategies (Vergassola *et al.*, 2007; Hein

685 & McKinley, 2012) is twofold. From an empirical perspective, the field needs to
686 move from trajectory data collection to hypothesis-driven experiments and com-
687 parative analysis to evaluate search tradeoffs and important variations of scale
688 across ecological contexts and species. From a modelling perspective, the field
689 needs to move from statistical curve fitting and model selection (Colding *et al.*,
690 2008; Smouse *et al.*, 2010; Jansen *et al.*, 2012; Reynolds, 2012, 2014) to exploring
691 the underlying universality among apparently different models (Frank, 2014).
692 Neither movement modelling discussions (Benhamou, 2007, 2014; Humphries
693 & Sims, 2014) nor high-throughput movement data (Humphries *et al.*, 2012;
694 Raichlen *et al.*, 2014) will be enough to disentangle pattern from process in an-
695 imal foraging. Hypothesis-driven and large-scale manipulative experiments are
696 required (Bartumeus, 2015).

697 Experiments do not need to be sophisticated. The perceptual scales, the
698 physiology, and the cognitive memory of an organism are not easy to control
699 but they can be manipulated or quantified to some extent in the laboratory.
700 Simple experimental setups with model organisms, for example, have been able
701 to show multi-scale properties both in bare and resourced landscapes (de Jager
702 *et al.*, 2011; Bazazi *et al.*, 2012; Salvador *et al.*, 2014; de Jager *et al.*, 2014;
703 Kölzsch *et al.*, 2015). In the future, the use of knock-out strains (e.g. *C.elegans*
704 mutants) and better empirical designs to exploit classic comparative approaches
705 of behavioural ecology (e.g. looking for gradients of information, motivational
706 states, or search regimes) will help producing a more comprehensive view of
707 foraging ecology, one including a behavioural response to uncertainty, which is
708 needed to transition between informed states.

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1002 **Box 1: Generalized Diffusion.**

1003 Diffusion can be intuitively described as the tendency for a group of particles
 1004 (driven by the random, irregular, and isotropic motion) to spread out in time,
 1005 and gradually occupy a larger area around their initial position (Okubo & Levin,
 1006 2001; Colding *et al.*, 2008). For the case of CRWs, a model largely discussed in
 1007 the ecological and the animal movement literature (Turchin, 1998; Colding *et al.*,
 1008 2008; Okubo & Levin, 2001; Viswanathan *et al.*, 2011; Méndez *et al.*, 2014b), it
 1009 is possible to obtain D as a function of speed and turning behaviour in isotropic
 1010 conditions, that is, equiprobable orientation of the spreading particles (Patlak,
 1011 1953; Lovely & Dahlquist, 1975; Dusenbery, 2009):

$$D(v, \alpha, \varphi(t)) = \frac{v^2 \langle t^2 \rangle \left[1 + \left(\frac{2\langle t \rangle^2}{\langle t^2 \rangle} - 1 \right) \alpha \right]}{2d \langle t \rangle (1 - \alpha)} \quad (4)$$

1012 where d is the space dimension, $\varphi(t)$ represents the distribution of flight times,
 1013 so $\langle t \rangle$ and $\langle t^2 \rangle$ are the first two moments of that distribution and represent a
 1014 measure of the directional persistence time (average time between turns). The
 1015 parameter $\alpha = \langle \cos \theta \rangle$ is the average angular correlation of an arbitrary distribu-
 1016 tion of turning angles θ ; then $\alpha = 0$ corresponds to the uniform distribution of
 1017 turning angles between 0 and 2π (see Supporting Information for a generalised
 1018 form of Eq. 4).

1019 For the case in which consecutive flights show no directional correlations
 1020 ($\alpha = 0$) and the persistence time is drawn from an exponential flight time dis-
 1021 tribution $\varphi_{corr}(t) = \langle t \rangle^{-1} e^{-t/\langle t \rangle}$ (so $\langle t^2 \rangle = 2\langle t \rangle^2$ is satisfied) D in the expression
 1022 above simplifies to

$$D_{corr} = D(v, 0, \varphi_{corr}(t)) = \frac{v^2 \langle t \rangle}{d}. \quad (5)$$

1023 Since D has dimensions of an area over time, one can intuitively interpret it
 1024 as the area explored by the particle (that is, the searcher) per unit time. Rigor-
 1025 ous random-walk calculations show that indeed the area covered by a random
 1026 walker in two dimensions is proportional to $D * t$, where t is the time (Yuste &

1027 Acedo, 1999).

1028 In the following we provide microscopic derivations of *anomalous* diffusion
 1029 coefficients involving two limiting cases discussed in the literature (Reynolds,
 1030 2012; Méndez *et al.*, 2014b, e.g.) movement with two characteristic scales or with
 1031 Lévy type of behaviour. For the simplest movement with only two characteristic
 1032 scales $\langle t_1 \rangle$ and $\langle t_2 \rangle$ whose corresponding weights are w and $1 - w$ one has
 1033 then $\varphi_{comp}(t) = \frac{w}{\langle t_1 \rangle} e^{-t/\langle t_1 \rangle} + \frac{(1-w)}{\langle t_2 \rangle} e^{-t/\langle t_2 \rangle}$. The *composite* diffusion coefficient
 1034 computed from Eq. 4 has the form

$$D_{comp} = D(v, 0, \varphi_{comp}(t)) = \frac{v^2 (w\langle t_1 \rangle^2 + (1-w)\langle t_2 \rangle^2)}{d(w\langle t_1 \rangle + (1-w)\langle t_2 \rangle)}. \quad (6)$$

1035 For a truncated Lévy flight characterised by a flight time distribution

$$\varphi_{enh}(t) = \frac{\mu}{t_{min}^{-\mu} - t_{max}^{-\mu}} t^{-1-\mu},$$

1036 with μ positive. The *enhanced* diffusion coefficient reads (including all possible
 1037 values of μ):

$$D_{enh} = \begin{cases} \frac{v^2}{2d} \left(\frac{1-\mu}{2-\mu} \frac{t_{max}^{2-\mu} - t_{min}^{2-\mu}}{t_{max}^{1-\mu} - t_{min}^{1-\mu}} + \frac{2\alpha}{1-\alpha} \frac{-\mu}{1-\mu} \frac{t_{max}^{1-\mu} - t_{min}^{1-\mu}}{t_{max}^{-\mu} - t_{min}^{-\mu}} \right) & \mu \neq 1, \mu \neq 2 \\ \frac{v^2}{2d} \left(\frac{1-\mu}{2-\mu} \frac{t_{max}^{2-\mu} - t_{min}^{2-\mu}}{t_{max}^{1-\mu} - t_{min}^{1-\mu}} + \frac{2\alpha\mu}{1-\alpha} \log \frac{t_{max}}{t_{min}} \right) & \mu = 1 \\ \frac{v^2}{2d} \left[(1-\mu) \log \frac{t_{max}}{t_{min}} + \frac{2\alpha}{1-\alpha} \frac{-\mu}{1-\mu} \frac{t_{max}^{1-\mu} - t_{min}^{1-\mu}}{t_{max}^{-\mu} - t_{min}^{-\mu}} \right] & \mu = 2. \end{cases} \quad (7)$$

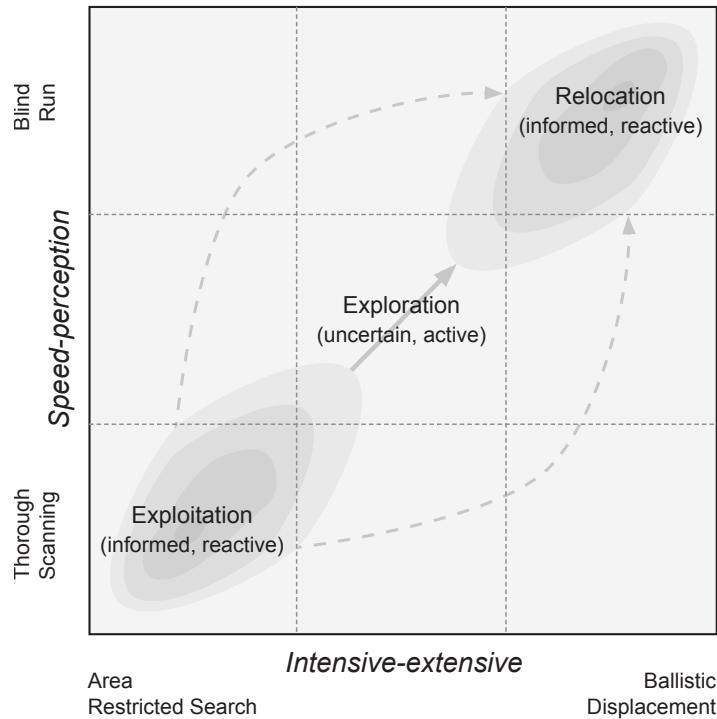


Figure 1: Diagram showing elementary tradeoffs delimiting a search state and informational space. The *speed-perception* tradeoff arises from the fact that high speed relocations improve the spreading capacity but reduce perceptual capabilities. The *intensive-extensive* tradeoff entails speed and turning and is related with the key tension between encountering nearby targets (intensive search mode) or being able to search more distant, and perhaps more profitable, areas (extensive search mode). While searching, different informational contexts force the decision-making on whether to stay (exploitative strategy) or leave (relocative strategy), leading to area-restricted search (ARS) and ballistic motion strategies respectively. Importantly, we suggest that changing from exploitation to relocation may often require a long behavioural transient, representing a much less informed exploratory state, where search tradeoffs govern the movement strategy. In this search behavioural space, the path across the diagonal (solid-line) looks more realistic and balanced in nature (both physically and biologically) than the paths crossing through the upper-left and the lower-right corner (dashed-lines).

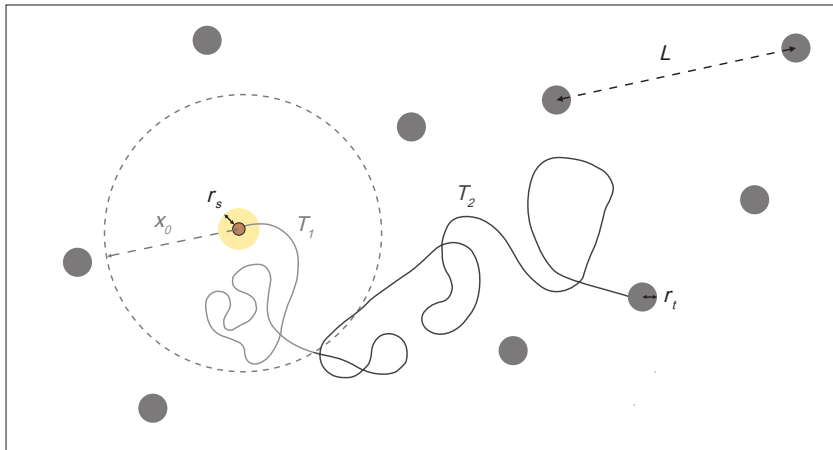


Figure 2: Depiction of key temporal and spatial scales involved in the computation of mean-first detection times. Grey filled circles represent targets and the smaller brown, filled circle represents the searcher. r_t and r_s are the size of the target and the perceptual scale of the searcher, respectively. L here represents the average distance between targets which can be associated to L in Eq. 3 and 2. We depict one single realization of the whole set of potential trajectories unfold by the searcher, and we show two relevant temporal phases, T_1 and T_2 , that can be associated to the different expectations of a searcher to get a target. T_1 is the mean time necessary to leave an empty area and approach a target. T_1 is a function of the spatial scale x_0 , which delimits the distance (grey dashed-circle area in two dimensions) that the searchers need to cross to reach the closest target, that is, the minimal distance required to initially spread out from an empty area. T_2 is the mean time needed to detect a target once the searcher trajectories are arbitrarily close to any target such that an *average* detection is possible.

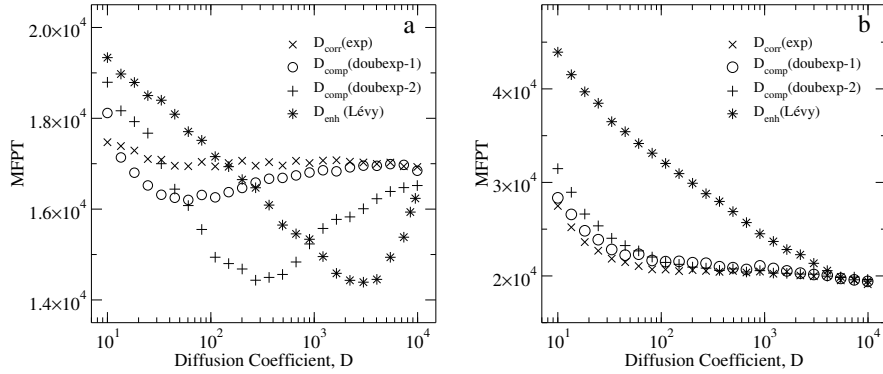


Figure 3: Mean First-Passage Time (MFPT) as a function of the diffusion coefficient for (a) asymmetric and (b) symmetric search conditions. Note that depending on the microscopic type of movement (exponential, double exponential, or truncated Lévy) the same macroscopic diffusion coefficient results in different MFPTs. For the asymmetric case, both enhanced (D_{enh}) and composite (D_{comp}) diffusion coefficients strongly decrease the MFPTs for some optimized range of values. In the asymmetric case, in general, the larger the number of movement scales involved in the diffusion coefficient the smaller the MFPT. Nonetheless, a well-parameterized double exponential (i.e. model doubexp-2) can mimic a truncated Lévy diffusion coefficient. For the symmetric case, the larger the diffusion coefficient the smaller the MFPT. In this scenario, incorporating multiple-scales (e.g. D_{enh} , D_{comp}) is not beneficial at all.

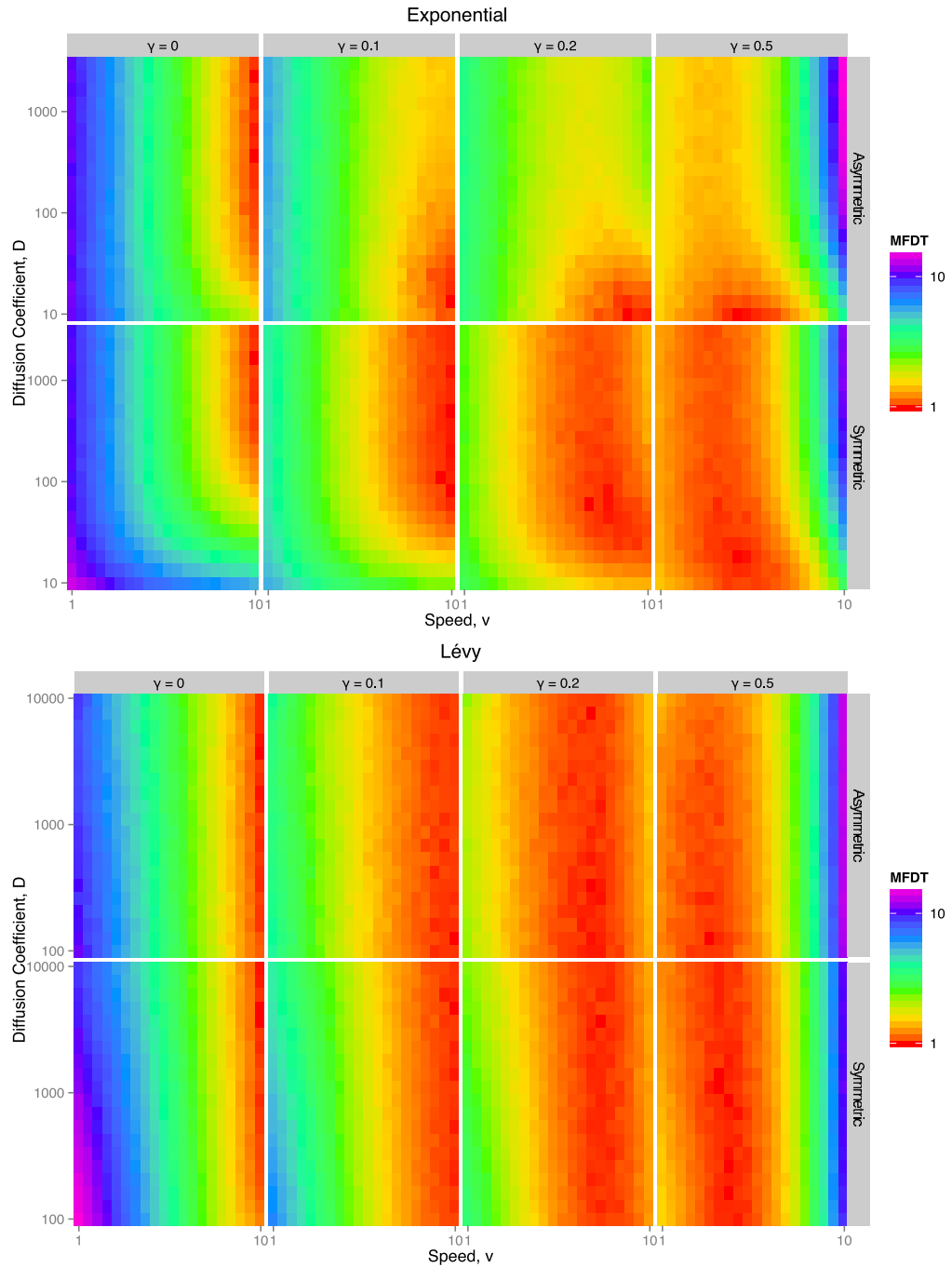


Figure 4: Mean First-Detection Time (MFDT) obtained as a function of the diffusion coefficient (D) and speed for exponential (upper panel) and truncated-Lévy (lower panel) distributions (in order to compute the effect of heavy-tailed relocations). For each distribution we also look for: (i) asymmetric and symmetric initial search conditions (in the first case the searcher can start moving from any point of the domain at random, while in the latter the searcher always start from any point within a distance $2R$ to a target, where $R = r_t + r_s$ is the sum of the detection scales or radius of the target r_t and the searcher r_s), (ii) different detection parameter values $\gamma = 0, 0.1, 0.2, 0.5$. The larger the γ the smaller the probability of detection.

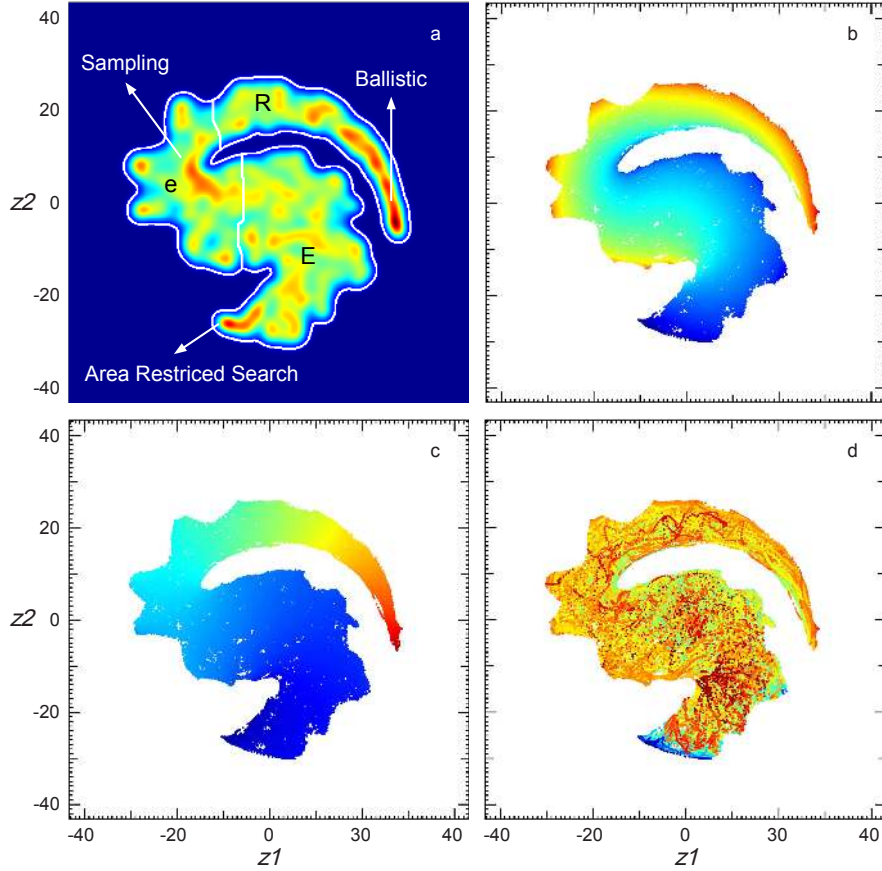


Figure 5: Quantitative analysis of the worm *Caenorhabditis elegans* long-term (90 minutes) search movement in a bare arena. Computation of the behavioural landscape based on a t-Stochastic Neighbouring Embedding (t-SNE) analysis (see Supporting Information). (a) Heat map of t-SNE landscape showing the emergence of three main domains (see Supporting Information) that can be associated to three search states (E=exploitation, e=exploration, and R=relocation). We also depict the dominant movement modes that characterize each of the search states: area-restricted search, sampling, and ballistic, respectively. Note, however, the complexity of the landscape and the presence of a hierarchical set of modes in each of the three large domains identified. (b,c,d) Heat maps of t-SNE space showing the values of the trajectory variables used as input features in the analysis: (b) the straightness index S , (c) the net displacement or effective velocity V , and (d) the mean travel velocity T .

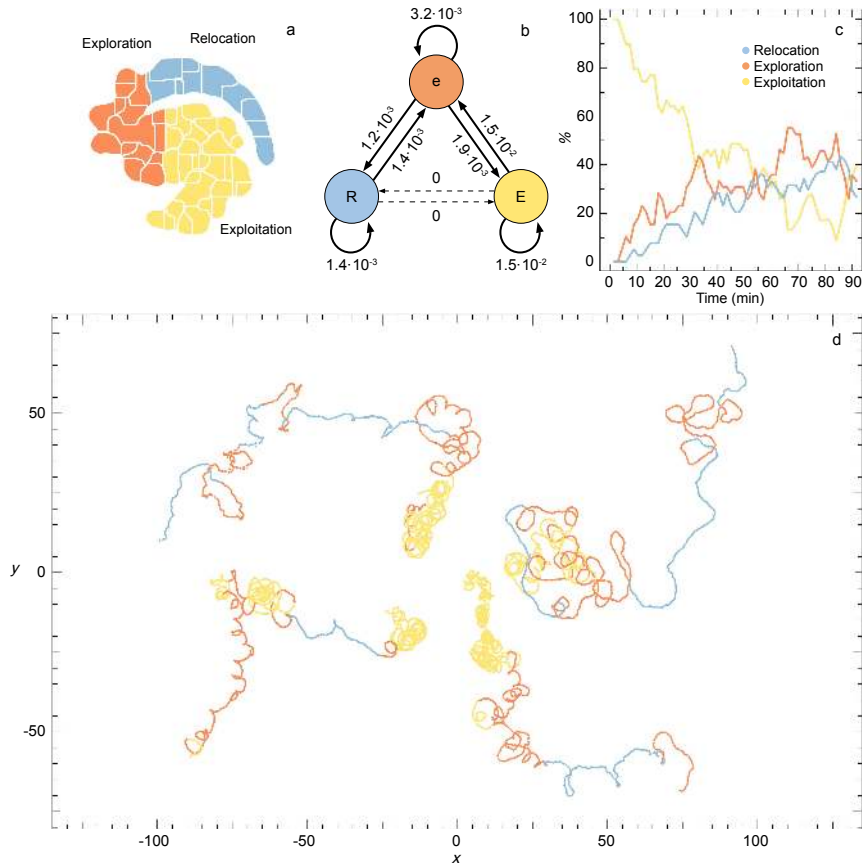


Figure 6: Quantitative analysis of the worm *Caenorhabditis elegans* long-term (90 minutes) search movement in a bare arena. Computation of the transition probabilities and temporal dynamics of the 3 search states (i.e. exploitation, exploration, and relocation). (a) The t-SNE landscape fully partitioned and highlighting the three statistically significant large domains identified, i.e. exploitation, exploration, and relocation (see Supporting Information). (b) Markov model and transition probabilities among the three emerging states (E=exploitation, e=exploration, and R=relocation) found in (a). (c) States' prevalences (probability of being in a given state) through time. (d) Example trajectories with the three states differentiated.

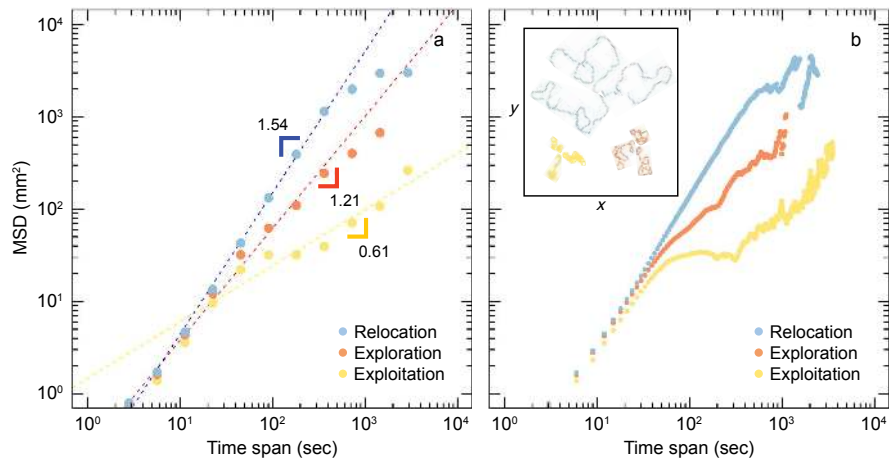


Figure 7: Mean square displacement (MSD) behaviour of the three search states found for *C.elegans* (see Figure 6). (a) Coarse-grained (logarithmic binning) behaviour of the MSD with time. Note the distinct long-term diffusive properties for each state, scaling exponents ranging from subdiffusion (< 1) to superdiffusion (> 1). (b) Highly-resolved behaviour of the MSD with time. Note the clear departures from pure diffusive behaviour, in particular, the presence of plateaus and small-to-large vertical fluctuations through time. Inset: Illustrative examples of trajectory segments showing the distinct looping behaviour observed in each of the three states. The steering control of *C.elegans* explains both the scaling exponents (a) and the strong departures from pure diffusion (b).

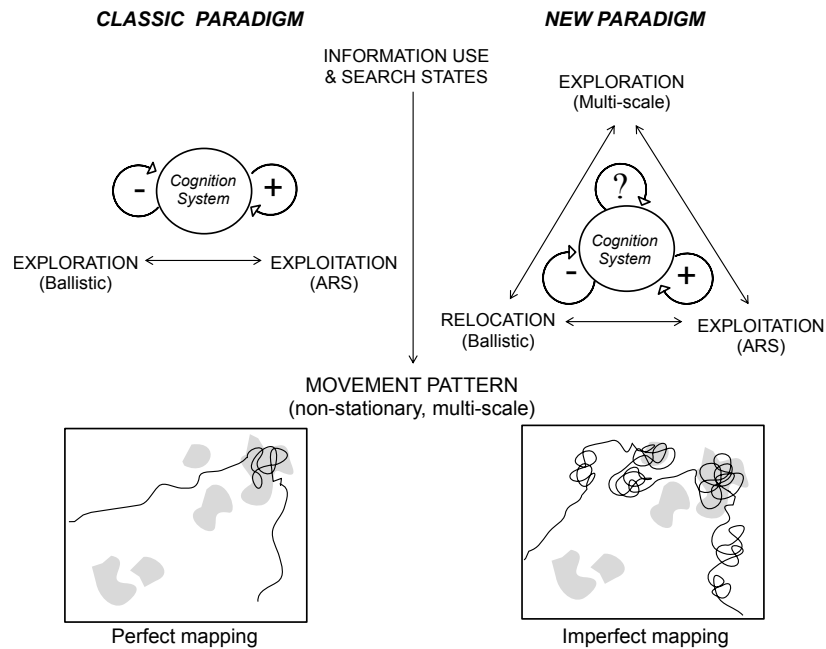


Figure 8: Depiction of the classic and the new foraging paradigm discussed, with two or three elementary motivational states (leading to three different movement modes) respectively. A general cognitive system establishes information fluxes and feedback with the external environment. The system measures information through its sensors, stores, processes, and interprets the information (with some internal modulation) to generate a positive, negative, or ambiguous reinforcement, which in turn trigger different behavioural attitudes or modes, each of them associated with a motor response. In the classic paradigm, the implicit assumption is that reactive behaviour governs. As a consequence, we should expect a perfect mapping between the movement of animals and the landscape structure. In the new paradigm, the implicit assumption is that animals are required to actively (and strategically) sample the environment, impairing a perfect mapping between movement patterns and landscape features.