IDEA AND PERSPECTIVE

Foraging success under uncertainty: search tradeoffs and optimal space use

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Abstract

Understanding the structural complexity and the main drivers of animal search behaviour is pivotal to foraging ecology. Yet, the role of uncertainty as a generative mechanism of movement patterns is poorly understood. Novel insights from search theory suggest that organisms should collect and assess new information from the environment by producing complex exploratory strategies. Based on an extension of the first passage time theory, and using simple equations and simulations, we unveil the elementary heuristics behind search behaviour. In particular, we show that normal diffusion is not enough for determining optimal exploratory behaviour but anomalous diffusion is required. Searching organisms go through two critical sequential phases (approach and detection) and experience fundamental search tradeoffs that may limit their encounter rates. Using experimental data, we show that biological search includes elements not fully considered in contemporary physical search theory. In particular, the need to consider search movement as a non-stationary process that brings the organism from one informational state to another. For example, the transition from remaining in an area to departing from it may occur through an exploratory state where cognitive search is challenged. Therefore, a more comprehensive view of foraging ecology requires including current perspectives about movement under uncertainty.

Keywords

Animal movement, composite correlated random walks, foraging ecology, Lévy walks, random walks, search behaviour.

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SEARCH BEHAVIOUR AND FORAGING ECOLOGY

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

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

Foraging animals experience different 'informational contexts' that lead to different motivational states and motor output (Morales *et al.* 2010). Active search behaviour (i.e. strategic sampling) is one such motivational state. More

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broadly, from a behavioural perspective, it is important to understand how animals transition back and forth from informed to relatively uninformed behavioural states. In other words, how do animals prioritise information when searching, capitalising on either exploitative or exploratory movement strategies (Vergassola *et al.* 2007; Hein & McKinley 2012). As suggested in McNamara *et al.* (2006), the optimal weight would depend on the specificity of the prior information and the quality of the current observations. From an evolutionary perspective, it is important to acknowledge that distinct selection pressures on search movement traits exist and depend on the informational context. Animals may adapt their search behaviour differently depending on whether the need is to unfold explorative strategies (e.g. fundamental information gathering, low information availability) or exploitative strategies (e.g. chemotaxis, area restricted search, or purposeful relocation movements to abandon a given area).

Search tradeoffs and information use

One might assert that there is a clear contradiction between the idea of *random* search (as probabilistic, uninformed movement) and the fact that organisms have evolved sensory and cognitive skills to exploit the environment. Nevertheless, biological details make this contradiction less apparent. Sensory and cognitive capacities are limited and thus organisms face situations of uncertainty when foraging. Random search theory can help us understanding the fundamental tradeoffs in these low-information situations and to identify the rules that lead to successful sampling.

In a random search process, three main elements govern encounter success: (1) speed, (2) turning patterns, and (3) perception (Méndez *et al.* 2014a). Here, we hypothesise that the combination of speed, turning and perception define two key compromises of random search (Fig. 1): (1) the *speed-perception* tradeoff where high speeds improve the spreading capacity but reduce perceptual capabilities (Dusenbery 1992; Campos *et al.* 2013), and (2) the *intensive-extensive* tradeoff, which is the fundamental compromise between being able to encounter nearby targets (intensive search mode) and at the same time find faraway targets (extensive search mode) in areas that might be more profitable (Raposo *et al.* 2011; Bartumeus *et al.* 2013, 2014; Méndez *et al.* 2014b).

Both the speed-perception and the intensive-extensive tradeoff define a bi-dimensional space where limiting cases can be identified (Fig. 1). In realistic biological scenarios, the two tradeoffs are not independent because they both depend on the organisms' speed: as speed increases, both perception and turning decrease. Therefore, for the case of biological searches, only a subset of the potential space depicted in Fig. 1 is accessible. In such a domain different informational contexts may coexist (represented as an information-availability landscape in Fig. 1). Indeed, the combination of two fundamental tradeoffs and the presence of informational gradients is believed to frame any search process, defining three fundamental search states: exploitation, exploration, and relocation (Fig. 1). Two of them (exploitation and relocation) are aligned with informed decision-making, for example, either staying in an area (leading to an area-restricted type of motion) or leaving out the area
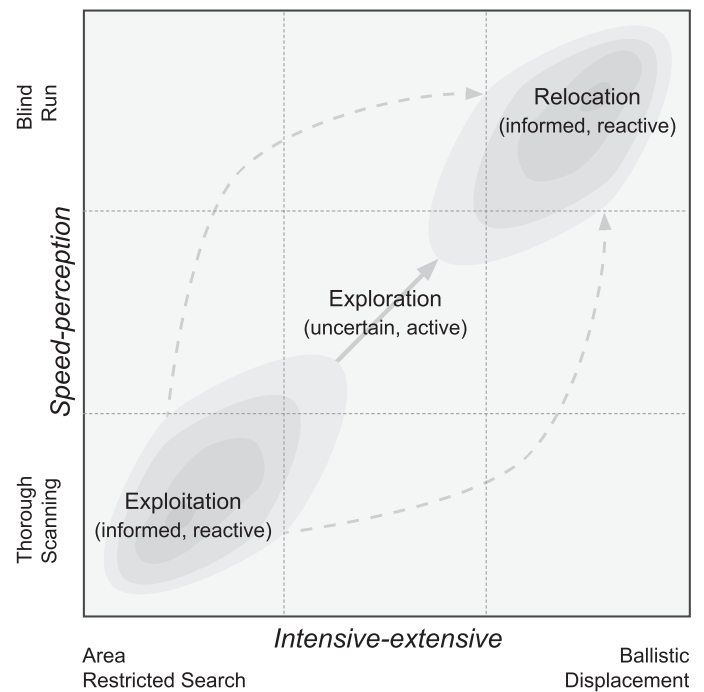

Figure 1 Diagram showing elementary tradeoffs delimiting a search state and informational space. The *speed-perception* tradeoff arises from the fact that high speed relocations improve the spreading capacity but reduce perceptual capabilities. The *intensive-extensive* tradeoff entails speed and turning 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 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).

(leading to straight-lined or ballistic motion). These two states involve two limiting behaviours represented in the lower-left and the upper-right corners of the search tradeoff space, where maximal information usability is also depicted (Fig. 1). Our working hypothesis is based in the principled guess that the transition between the stay-leave decisions (exploitation vs. relocation) often requires a third state (exploration) that leads to complex movement patterns aimed at gathering more information. Many behavioural transitions may exist between stay-leave states (i.e. paths transiting from the lower-left to the upper-right corner in Fig. 1), but only paths around the diagonal adequately balance the two tradeoff conditions, unfolding the most effective sampling movement possible. Paths crossing the upper-left and the lower-right corners (Fig. 1) involve either too blind or too slow exploratory behaviours, respectively, suggesting suboptimal and less biologically plausible stay-leave transitions.

Figure 1 redefines search as a ternary (i.e. exploitation-exploration-relocation) instead of a binary (i.e. exploitation-

exploration) process (Hills *et al.* 2015). Indeed, we suggest that the exploration and the relocation states are erroneously unified and that the understanding of the transition dynamics between the three states identified here is fundamental for the comprehensive inclusion of search behaviour in foraging ecology. In particular some questions are: (1) how are search states associated with movement behavioural modes? (2) does the exploration state represent a short or a long transient between the two more informed states? (3) what are the elementary constraints and optimisation rules governing the exploration state? (4) which motion patterns emerge during the exploratory state?

Guided by these ideas (Fig. 1), we place current random search theory into an eco-evolutionary perspective. First, we identify key spatiotemporal scales of the search process that need to be considered to understand the search behaviour of the organism. Second, we show that not only the total amount of area covered but also how the area is filled (i.e. space use) is crucial to optimise a random search strategy. Third, we evaluate the key role of speed and diffusion in the speed-perception and the intensive-extensive tradeoffs by running simulations covering a wide range of the key parameters. Fourth, we analyse empirical trajectories of *Caenorhabditis elegans* in a specific search context, showing why biological details (i.e. information-processing, internal states, and motor constraints) are important for the understanding of search behaviour in the context of foraging ecology. Finally, we suggest further experiments to explore the usefulness and validity of the proposed new search paradigm in general foraging-ecology research.

FACTORING THE TIME TO FIND A TARGET

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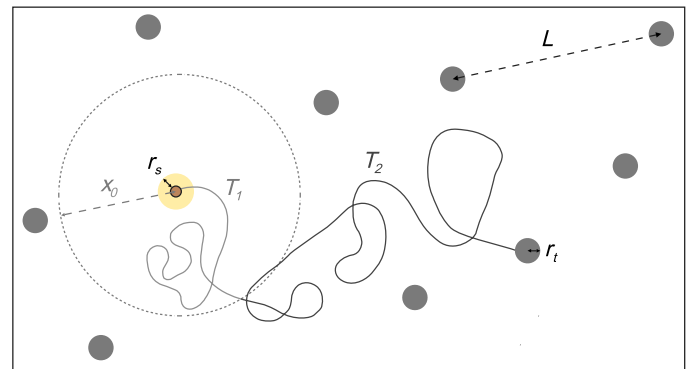

Figure 2 Depiction of key temporal and spatial scales involved in the computation of mean-first detection times. Grey filled circles represent targets and the smaller brown, filled circle represents the searcher. r_t and r_s are the size of the target and the perceptual scale of the searcher, respectively. L here represents the average distance between targets which can be associated to L in eqns 2 and 3. We depict one single realisation 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.

To calculate MFDTs one must consider (see also Box 1), (1) the movement parameters: speed v, angular correlation α, and 'flight time' distributions $\varphi(t)$, where t represents jump or displacement durations. These parameters ultimately define a diffusion constant $D(v, \alpha, \varphi(t))$, (2) detection parameters: a probability of detection as a function of speed $p(v)$, and (3) boundary conditions: a typical domain size (characterised by the average mean free path between targets L), which also determines the density of targets, a generic perceptual scale defined here as the sum of the searcher perceptual scale and the target size $R = r_s + r_t$, where $R \ll L$, and an initial distance x_0 of the searcher to the closest target, which represents the minimal distance required to leave the empty area within the search domain.

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

$$\langle T \rangle = T_1 + T_2, \tag{1}$$

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 process is divided into two temporal phases: (1) the mean time needed to leave the empty area defined by the distance to the closest target, during which the probability of detecting a target is zero or negligible on average, i.e. T_1, and (2) the mean time needed to detect a target, once the searcher probability of detection is non-negligible on average, that is, T_2.

During the approaching phase (i.e. T_1), the average detection is zero and the distance from the initial position to the closest target x_0, and the type of diffusive process D are the limiting factors determining the probability to reach a target.

The probability to detect targets in the T_2 phase, depends mostly on the speed v and the perception ability as a function of speed $p(v)$. Motion in T_2 may include subsequent back-and-forth movements away and towards the targets so it might appear puzzling that T_2 does not depend explicitly on D. The explanation for this is that when directional persistence has a single (or predominant) characteristic scale it plays an ambivalent role that neutralises the effects of the diffusion coefficient D in the term T_2. Whenever the searcher moves towards the target, an increase in directional persistence (or characteristic flight time) facilitates encounters with targets. However, if it is in the wrong direction, the same increase may impair encounters with relatively close targets. The general result is that whenever D is governed by one single characteristic flight time the effect of D on T_2 is cancelled out (for further details see the Supporting Information). Nonetheless, the introduction of multiple persistence scales (or flight times), either due to the effect of heavy tails or multimodal distributions solves this limitation and introduces the possibility of further search optimisation (Bartumeus *et al.* 2014; Campos *et al.* 2015b). Other mechanisms not explored here can also lead to non-monotonic effects of directional persistence in first-passage times (Tejedor *et al.* 2012).

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

If one extends the random search problem to systems with an arbitrary number of dimensions d, the computation of the MFDT needs an additional characteristic scale, the target size (also interpreted as an effective detection distance in Méndez *et al.* (2014a)). This is essentially defined as the characteristic distance between the target and the searcher so that on average target detection becomes significant. Note that in one-dimensional systems the target can be considered as a point (zero effective size) since the random walker will pass sooner or later through that point with probability 1. The latter is not true in higher dimensional systems. For a random walk with persistence modelled as a correlated random-walk (CRW) starting at an arbitrary position x_0 of a d-dimensional spatial domain with a mean-free path between targets L, the equation for the MFDT can be written as (Campos *et al.* 2013):

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

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

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

Note that both eqn 3 and eqn 2 preserve the scaling and interpretation made in Fig. 2 for T_1 and T_2, such that (1) the size of the target, which is essentially related to the detection probability, only appears in T_2 but not in the approaching time T_1, (2) the diffusion coefficient D is present in T_1 but not in T_2 (see Supporting Information for further insights), and (3) the time T_1 always fulfils the diffusive scaling $\sim L^2$ while the detection time T_2 scales as L^d, since the time to detect the target in a stationary situation is proportional to the empty volume of the system (or target density).

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

These simple models (eqns 3 and 2) emphasise that in a search process, the spacing and distribution of resources are relative to searcher position and perceptual scales (i.e. x_0/L, R) and matter to the extent they modify the searcher encounter statistics (average and variation of the encounter time intervals). Nonetheless, an organism-centred view of the resource spacing is notoriously difficult to capture in a single meaningful metric (Lima & Zollner 1996). The key temporal

Box 1 Generalised diffusion

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

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

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

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

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

Since D has dimensions of an area over time, one can intuitively interpret it as the area explored by the particle (that is, the searcher) per unit time. Rigorous random-walk calculations show that indeed the area covered by a random walker in two dimensions is proportional to $D \times t$, where t is the time (Yuste & Acedo 1999).

In the following, we provide microscopic derivations of *anomalous* diffusion coefficients involving two limiting cases discussed in the literature (e.g. Reynolds 2012; Méndez *et al.* 2014b) movement with two charactersitic scales or with Lévy type of behaviour. For the simplest movement with only two characteristic scales $\langle t_1 \rangle$ and $\langle t_2 \rangle$ whose corresponding weights are w and $1 - w$ one has 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 computed from eqn 4 has the form

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

For a truncated Lévy flight characterised by a flight time distribution

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

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

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

and spatial scales identified in the search model are linked to the organisms perceptual scales in a complex way. The connection is not only dependent on the densities and distribution of resources and consumers, but also on cue-related spatial gradients, physical topography, forager motivation, history of experience or age and social processes. Clearly, the framework presented here is limited in the sense of compacting all these relevant aspects into one single metric, the searcher-to-target nearest distances.

DIFFUSION AND SPACE USE

In principle, it may seem that the ultimate goal of search is to explore more territory in less time. However, search efficiency measures success in finding targets, not in covering space; therefore, despite the fact that the maximisation of space coverage is important, and in many occasions correlates positively with search efficiency, it is not always the best strategy. If near and faraway targets are to be found, then the

intensive-extensive tradeoff emerges, and one finds that the search efficiency does not depend strictly on the amount of territory explored per unit time (i.e. D) but on *how* this territory is explored to find the target. In particular, persistent motion alone is not enough to efficiently optimise both close and distant target encounters (Bartumeus *et al.* 2005).

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

In our example (Fig. 3), the increase in D along the x-axis is achieved by keeping the velocity constant and only changing the parameters that affect the flight time distribution. Note that for a given spreading capacity (i.e. D) the MFPT changes depending on whether the microscopic movement leads to normal or anomalous diffusion (Benhamou 2014; Seuront & Stanley 2014; Bartumeus 2015). Different mechanisms leading to anomalous superdiffusion have been suggested, either through enhanced (D_{enh}) or composite diffusion

(D_{comp}) (Bartumeus *et al.* 2005, 2014; Benhamou 2007; Raposo *et al.* 2011; Reynolds 2012) (see also Box 1). Importantly, both types of non-Brownian diffusivity decrease the MFPT (i.e. T_1 of eqn 1) at intermediate D's. Also, the search efficiency improves compared to a simple diffusive process, driven by an exponential distribution of flight times (eqn 5) and also to straight-lined motion. Both D_{enh} and D_{comp} may result in a similar search efficiency and may be better than D_{corr}, where single-scaled persistence or characteristic flight times is incorporated. Hence, Fig. 3 confirms that the optimal balance between intensive-extensive search cannot be unequivocally determined by D but depends on the microscopic details of the turning patterns, in particular the inter-turn time or flight time distribution $\varphi(t)$. Turning patterns balance out the capacity of the searcher to move away and come back from/to the target. Such a balance requires multi-scaled (and far from Gaussian) movement patterns (Bartumeus *et al.* 2014; Méndez *et al.* 2014b). The latter can be achieved either by generating a mixture of D's with different Gaussian parameters for speed and flight times (D_{comp}), or by incorporating heavy-tailed speed and flight time distributions (with a slower decay than Gaussian but finite moments) within one single D (D_{enh}). Currently, defining the generative mechanisms leading to anomalous dynamics (departures from normal diffusion) is an active field of research (Benhamou 2007; Heisenberg 2009; Brembs 2011; Bazazi *et al.* 2012; Campos *et al.* 2014; de Jager *et al.* 2014; Salvador *et al.* 2014; Wearmouth *et al.* 2014; Reynolds 2015).

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

SEARCH OPTIMISATION

While the discussion in the previous section illustrates the crucial scales and tradeoffs influencing search processes, they may
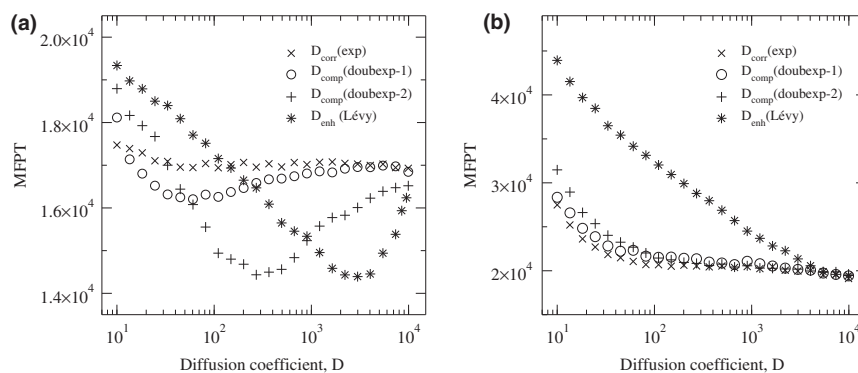

Figure 3 Mean first-passage time (MFPT) as a function of the diffusion coefficient for (a) asymmetric and (b) symmetric search conditions. Note that depending on the microscopic type of movement (exponential, double exponential, or truncated Lévy), the same macroscopic diffusion coefficient results in different MFPTs. For the asymmetric case, both enhanced (D_{enh}) and composite (D_{comp}) diffusion coefficients strongly decrease the MFPTs for some optimised 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-parameterised 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.

give the false impression that the two fundamental search trade-offs (i.e. intensive-extensive, speed-perception) can be optimised independently. This is not true since both perception and the diffusion constant D are affected by the searcher speed. Hence, a unique global optimum that minimises the search time can be determined, but requires a complete parameterisation of the problem that includes search behaviour (movement and perception) and the landscape properties.

Here we perform a comprehensive, quantitative analysis. The searcher moves within a domain that is large enough so boundary effects are negligible (large L with periodic boundary conditions), and flights are at constant speed separated by turning events (uniformly random direction). Target density is represented by $1/L^d$, where d is the spatial dimension. We analysed two qualitatively different search regimes. In the symmetric regime, the searcher starts moving from any point in the whole domain drawn from a uniform distribution. This scenario reflects an average distance towards the closest target of the order of the domain size, representing a homogeneous landscape from the perspective of the searcher. In the asymmetric regime, the searcher starts from any point drawn from a Gaussian distribution with variance $\sigma = 2R^2$ centred at a given target position, 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. As $R \ll L$ the typical scales of the distance to the close-by ($2R^2$) and faraway (L) targets are different, representing a heterogeneous landscape from the searcher perspective.

The whole spectrum of possible search strategies depicted in Fig. 1 has to be explored in order to look for global optimal compromises. We characterised the intensive-extensive tradeoff through the diffusion coefficient D, computed from the microscopic parameters (see Box 1), and the speed-perception tradeoff using the speed v along with the speed-dependent factor $e^{-\gamma v}$, which determines the probability of detecting the target after passing over it ($\gamma > 0$). In these simulations, we consider that perception occurs once per flight, instead of considering a continuous process. While alternative choices of parameters would be possible, the choice of D and v is appropriate as it encompasses the whole decision-making set of possibilities that the searcher has available to improve its strategy. Fig. 4 compares the MFDT obtained as a function of the diffusion coefficient (i.e. varying $\varphi(t)$ and keeping speed as a constant), and speed for: (1) exponential and truncated-Lévy flight time distributions (a paradigmatic heavy tail distribution, common in empirical observations, and easy to handle when computing the effect of heavy-tailed flight times), and (2) different detection parameter values $\gamma = 0, 0.1, 0.2, 0.5$ (in order to determine the effect of perceptual capabilities, the larger the detection parameter γ the smaller the probability of detection), and (3) two types of initial conditions, leading to two different search regimes (Raposo *et al.* 2011; Bartumeus *et al.* 2013, 2014). In our simulations, we are not considering any energetic cost related to speed (e.g. speed as a function of energy cost or speed limits), which could have additional effects on search efficiency beyond the effects of the speed-perception tradeoff explored here.

For the exponential flight time distribution (Fig. 4, upper panel) and for *easy detection* conditions ($\gamma = 0, 0.1$), the global optimum strategy (low MFDTs) lies in the region of a large diffusion constant (D) and high speed (v). The result is qualitatively similar for both search regimes (symmetric or asymmetric). Concordantly with Reynolds & Bartumeus (2009), as perception error increases and target detection becomes less probable, the global optimum is displaced towards smaller values of speed (the slow, scanning limit) and smaller values of D (intensive search limit) compared to the case with perfect detection. Noticeably, the confinement of the optimal solution (low MFDT values) at small values of D is stronger in the asymmetric than in the symmetric regime. So, searchers strongly constrained by perception will benefit from using moderate speeds and intensive strategies in order to revisit places several times to balance possible detection failures. This solution is more relevant when nearby targets exist, and importantly, we have checked numerically that this tendency is independent of the details of the detection process (e.g. using other functions $p(v)$ or introducing more complicated movement patterns which include pauses). So the necessity for slowing down and enhancing revisits (intensive search) when perception is impaired seems to be a rather general and robust conclusion and may only depend quantitatively from certain details on how the perception process is implemented.

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

SEARCH BEYOND PHYSICS: AN EXPERIMENT WITH NEMATODES

Discerning among potentially different search states and characterising specific movement modes associated to them (Fig. 1) is a challenging task. Often, it results controversial whether organisms perform active sampling or they are merely reacting to local environmental cues. Nonetheless, by displacing an organism from a rich- to a poor-resource environment, so that both the quantity and the quality of available information changes abruptly, one can investigate how organisms adjust their search behaviour to low information conditions (Bazazi *et al.* 2012; Salvador *et al.* 2014; Seuront & Stanley 2014). In resource-rich environments, organisms are well-fed and surrounded by resources but when displaced to a resource-poor and cue-less environment animals start to experience a radically
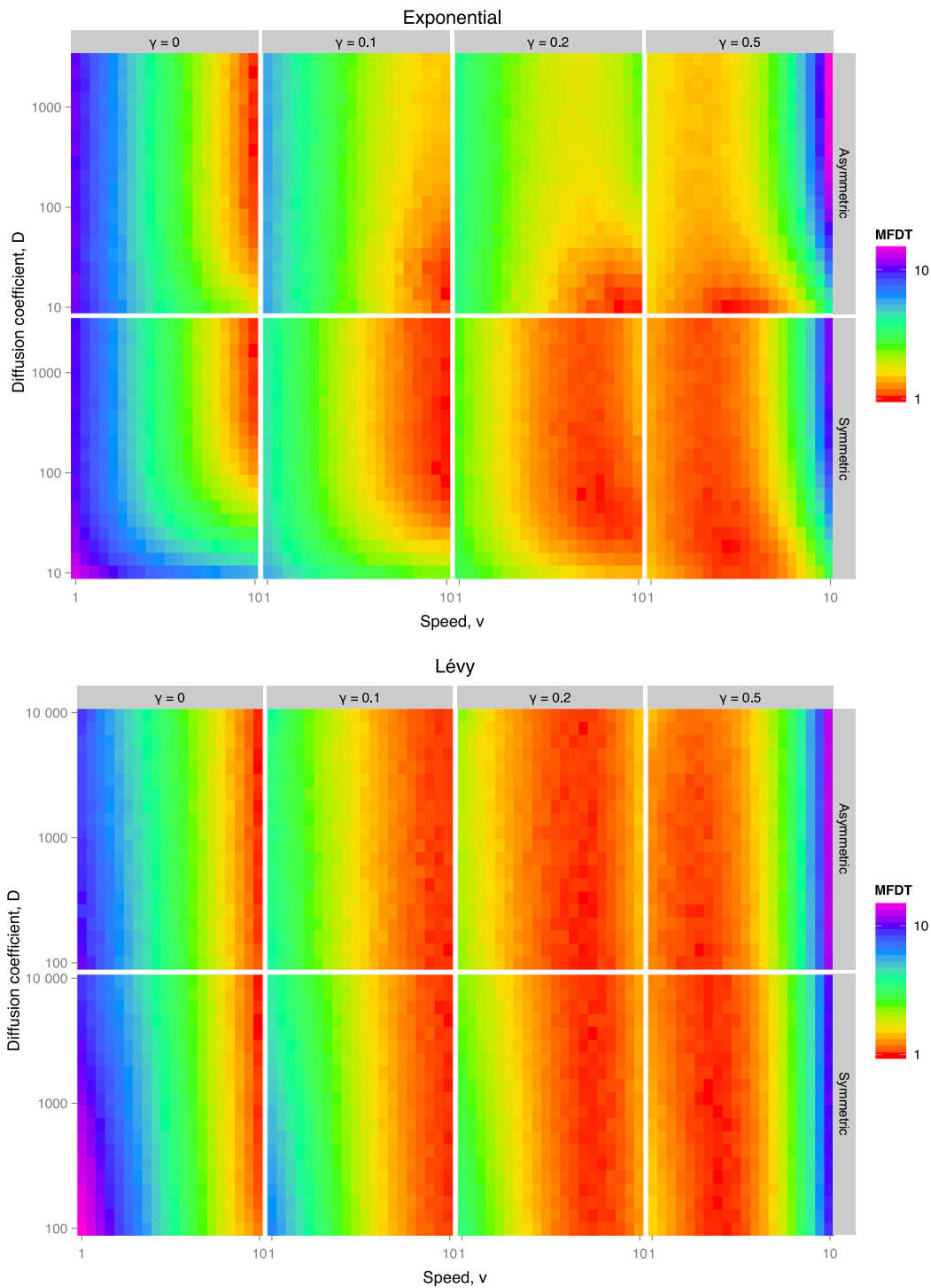
Figure 4 Mean first-detection time (MFDT) obtained as a function of the diffusion coefficient (D) and speed for exponential (upper panel) and truncated-Lévy (lower panel) distributions. For each distribution we also look for: (1) asymmetric and symmetric initial search conditions. In the first case the 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, (2) different detection parameter values $\gamma = 0, 0.1, 0.2, 0.5$. The larger the γ the smaller the probability of detection.

different situation. In such cases, one would expect organisms to *actively* try to gather information near their initial position before deciding to leave. A crucial aspect is whether the transition between exploitation (i.e. remaining in an area) and relocation (i.e. departing from) is determined by exploratory movements, governed by the fundamental tradeoffs and the optimisation mechanisms explained in the above Sections, or alternatively, it is a fast transition governed by relatively

informed movement. To address this question we perform this type of experiment with the nematode *Caenorhabditis elegans*.

We place, one at a time, 39 *C. elegans* individuals (well-fed on a bacteria lawn for several days) onto a bare agar plate (zero food) of 24.5×24.5 cm^2 at a homogeneous temperature of 21 °C, and track their movement at high-resolution (32 Hz) for about 90 min. In this experimental setup the environment of the worm is carefully controlled, so its movements are mainly determined by the animal's internal state (e.g. starvation level or memory of the previous conditions) and not to any environmental cues (e.g. temperature or chemical gradients).

Search is a non-stationary behavioural process

Our working hypothesis is that foraging organisms are confronted with different motivational states and information-availability contexts that modulate movement behaviour (Fig. 1). Despite our dataset covers a wide range of scales,

one must always be cautious when inferring true behavioural processes from movement data.

We characterise *C. elegans* movement on the basis of three variables including: straightness index (S), net displacement D (or effective velocity, V), and mean travel velocity (T) (see Supporting Information). We use t-Stochastic Neighbouring Embedding (t-SNE) (Berman *et al.* 2014) and classic Hidden Markov Modelling to segment these trajectories into different movement modes (see Supporting Information). Our analysis reveals a complex behavioural landscape delimited by three statistically significant domains or regions (Fig. 5a). Each domain is characterised by a dominant (and differentiated) movement mode among a hierarchical set. The emergence of three large domains in the behavioural landscape suggests the presence of three motivational search states, namely, exploitation, exploration and relocation, which in turn, are characterised by three dominant movement modes: area-restricted search (ARS), sampling, and ballistic-like motion respectively (Fig. 5a). Based on these empirical results, we hypothesise that search behaviour is governed by three motivational states
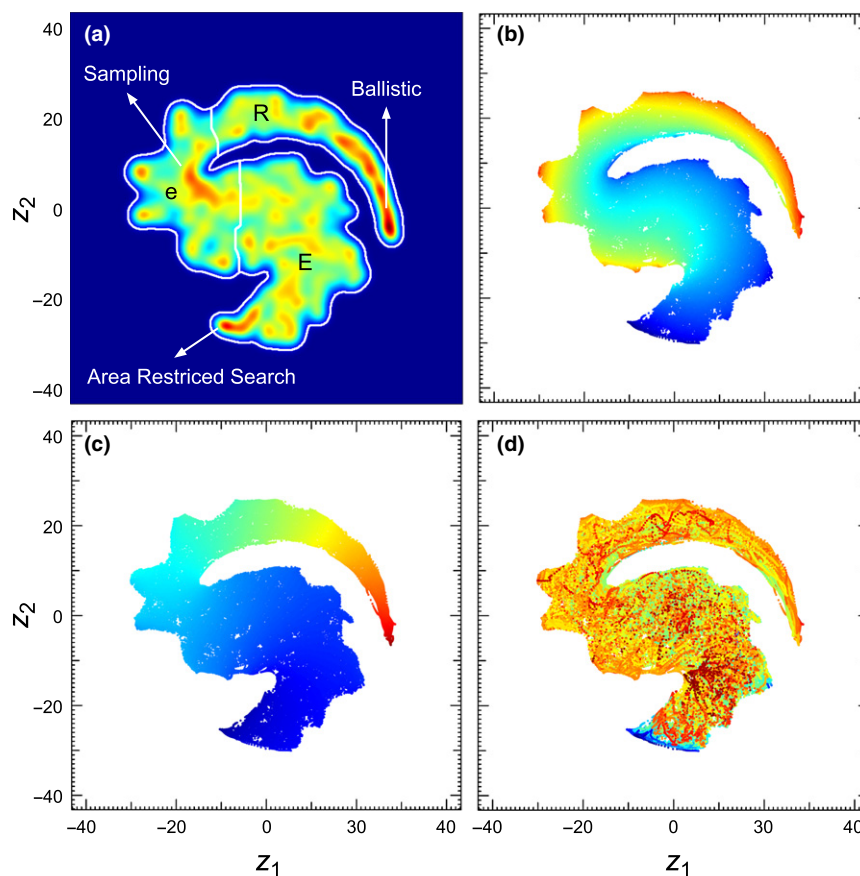

Figure 5 Quantitative analysis of the worm *Caenorhabditis elegans* long-term (90 min) search movement in a bare arena. Computation of the behavioural landscape based on a t-Stochastic Neighbouring Embedding (t-SNE) analysis (see Supporting Information). z_1 and z_2 are the two dimensional embedding variables of the behavioural landscape. (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 characterise 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.

that modulate the propensity by the organism of being in one or another movement mode. To interpret better the behavioural landscape (i.e., the main domains and movement modes), we depict the values of each of the input variables (see Supporting Information) on the landscape (Fig. 5b,c,d). In particular S and V can be considered rough surrogates of the intensive-extensive and the speed-perception tradeoffs. Its marked gradation (Fig. 5b,c) ensures that the three dominant movement modes represent different tradeoff compromises. Compared to S and V, the mean travel velocity T is more heterogeneously distributed across the landscape. The smallest T's are strongly associated to area-restricted search behaviour, but small and large T's can locally co-occur elsewhere in the behavioural landscape.

Finally, we use the results obtained from the t-SNE segmentation procedure to feed a 3-state Markov-chain to model the transitions and the overall temporal dynamics of the three search states. We find that the exploitation and the relocation states do never occur consecutively in time but they are rather linked through a differentiated exploratory state (Fig. 6b). In addition, the state's prevalence dynamics shows a gradual shift from exploitation to relocation, with an intermediate

phase (around minute 70 of the experiment) governed by exploration (Fig. 6c). These results are also confirmed when directly modelling the data with 3-state Hidden Markov Models (see Supporting Information).

As in Salvador *et al.* (2014), in this experiment the memory of the previous environment (culture plentiful of bacteria) seem to anchor the animal for about 30 min around its initial position. Therefore, in this case, ARS is not directly driven by chemotaxis. The exploitation state must be the result of the memory (*sensu latu*) of past resource availability, which may progressively relax due to cumulative failures in sensing resources. In *C. elegans* ARS is maintained mainly using a special type of turn known as pirouettes (Pierce-Shimomura *et al.* 1999; Ohkubo *et al.* 2010; Salvador *et al.* 2014). Once the resource memory or expectation has dropped, the worm is engaged in an exploratory process aimed at effectively expanding the search area. At this stage, it combines pirouettes with straight-lined crawls, and multi-scale looping behaviour, drifting away from the initial area. Finally, after about 30 min in the exploratory mode, the worm performs sustained straight-line motion, to the extent that its steering control allows it, suggesting an aim to *relocate* or *leave* the area
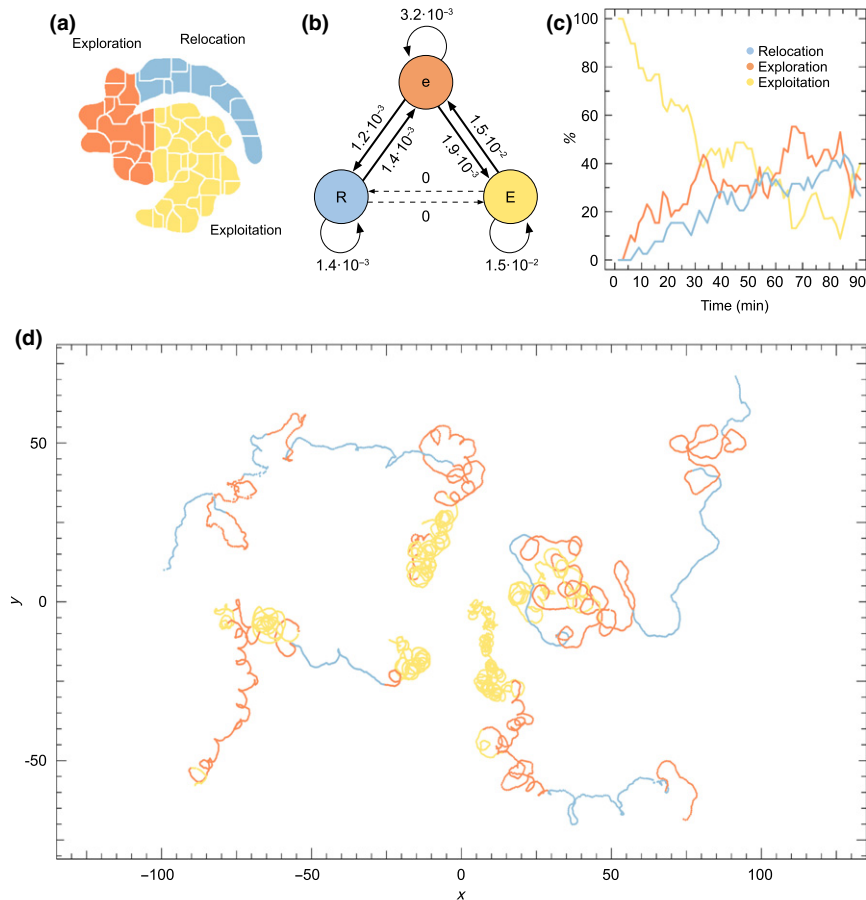

Figure 6 Quantitative analysis of the worm *Caenorhabditis elegans* long-term (90 min) search movement in a bare arena. Computation of the transition probabilities and temporal dynamics of the three search states (i.e. exploitation, exploration, and relocation). (a) The t-SNE landscape fully partitioned 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.

(Fig. 6d). All in all, in well-fed *C. elegans* individuals "stay-leave" decisions involve a transition from ARS to ballistic-like movement that spans about 1 h (Fig. 6c). These type of transitions are species specific, e.g. well-fed locusts changed from intensive to extensive search much more progressively, in the course of 6 h (Bazazi *et al.* 2012). Ballistic and fast motion is the optimal strategy for an organism moving in a bare arena, when all targets are faraway (Bartumeus *et al.* 2005, 2014), but organisms need a time and perform specific motion to figure out this situation.

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

The results revealed that *C. elegans* produces complex locomotory patterns that are not directly related to environmental fluctuations or resource density (Avgar *et al.* 2011; de Jager *et al.* 2014). Our data confirms the results in Salvador *et al.* (2014) and Calhoun *et al.* (2014), i.e. the transition from ARS to ballistic-like motion in *C. elegans* is not fast nor simple but it entails a long and complex transient period. Therefore, this search can be described as a non-stationary behavioural process that drives the worm from the decision of remaining in the area to the decision of departing from it, through a relatively long intermediate stage.

Behavioural details govern search diffusion

Diffusion is a relevant metric to understand biological search capacity (see Section 'Diffusion and Space Use') but often organisms' movement depart from the idealised microscopic descriptions of diffusion (Méndez *et al.* 2014b). In this sense, the search movement of *C. elegans* is not only *non-stationary* but it clearly departs from the simple *run-and-tumble* random-walk model (Stephens *et al.* 2010). Indeed, *C. elegans* performs many different types of *turns*, each producing different changes in angular direction, and its *runs* are not simple straight paths but rather curvilinear trajectories (Izquierdo & Beer 2015), with a broad distribution of curvatures.

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

The exploitation, exploration, and relocation states reveal distinct space use, based on different looping motifs and
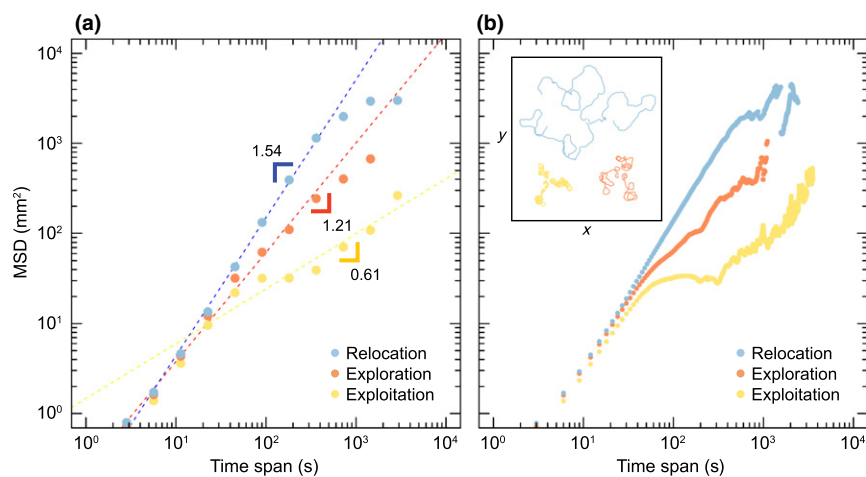

Figure 7 Mean square displacement (MSD) behaviour of the three search states found for *Caenorhabditis elegans* (see Fig. 6). (a) Coarse-grained (logarithmic binning) behaviour of the MSD with time. Note the distinct long-term diffusive properties for each state, scaling exponents ranging from subdiffusion (< 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).

diffusivities. At the beginning of the experiment, the exploitation phase entails tight loops that slowly drift and overlap each other (Fig. 7b, inset). This looping behaviour leads to a strong subdiffusive regime ($\alpha < 1$, see Fig. 7a) and to a complex MSD curve that plateaus for a range of scales and then subsequently increases showing strong fluctuations at the end (Fig. 7b). During exploration, the total area covered is similar to that of the exploitation state but the coverage occurs about four times faster due to marginally super diffusive behaviour ($\alpha \geq 1$, Fig. 7a). In this state, loops are loose and combined with straight-lined segments (Fig. 7b, inset). When relocation is taking place the worm generates wide loops (Fig. 7b (inset), also called open arcs in Salvador *et al.* (2014)), which generate superdiffusive behaviour ($\alpha > 1$, Fig. 7a). In general, the steering control of *C. elegans* cannot avoid systematic orientational biases (Izquierdo & Beer 2015), impairing ballistic motion in the long-run. In the three states, the long-term MSD behaviour converges to (sub)normal diffusion (Fig. 7a). A more detailed picture of the MSD behaviour (Fig. 7b) reveals that the MSD fluctuations systematically increase through time due to the long-return times to previously visited areas.

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

TOWARDS A COMPREHENSIVE VIEW OF FORAGING

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

Here we have made an explicit connection between classic macroscopic parameters (e.g. diffusion, average speed), mesoscopic movement properties (e.g. directional persistence, flight distributions), target density and distribution (e.g. domain size, symmetric/asymmetric regimes), and search efficiency. We have used both analytical and numerical methods to investigate how movement processes operating at different scales affect search efficiency. The theoretical results suggest that (1) the organism's exploratory behaviour may involve two critical temporal phases (i.e. approach and detection), mostly associated with two basic search tradeoffs (i.e. intensive-extensive, speed-perception) and that the (2) organisms search behaviour should be inherently multi-scaled to balance out the intensive-extensive and the speed-perception tradeoff. Random search theory, however, should be considered just the basic groundwork for understanding biological search

phenomena. Other layers need to be added such as the effects of learning, memory, as well as biological details related to motor and cognitive constraints in organisms.

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

It has been hypothesised that information processing, modulated by some internal state (hunger, fear, etc.), triggers behavioural modes and the transitions among them (Morales *et al.* 2010). In the most parsimonious (classic) view, foraging involves only two basic motivational states: (1) exploiting the regions with available target information, and (2) relocating (leaving) to new exploitable areas. The combination of these two states can lead to multi-scale (complex) movement behaviour only if the landscape itself or the cues followed by the animal have multi-scale properties (Benhamou 2007, 2014; Schick *et al.* 2008). If perfectly informed, such motivational states would generate movement modes closely matching the landscape or its associated cues (Fig. 8). Clearly, this classic paradigm is not enough to explain the *gradual* behavioural transition from exploitation to relocation often observed and characterised by complex movement behaviour. We argue that there is the need to consider at least one more motivational state (and movement mode) between the informed states, which will be related to exploration under uncertainty.

In this new paradigm, a richer behavioural repertoire of foraging movements would emerge from the transitions between three rather than two motivational states (Fig. 8), corresponding to the exploitation, relocation, and exploration states. In the classic model, positive and negative target cues trigger the exploitation and relocation states, respectively. Here we suggest that ambiguous or unreliable information can trigger active sampling and exploratory behaviour. Following the previous sections such an exploratory state would have evolved to deal with the elementary search tradeoffs, and would have resulted in multi-scale motion patterns that do not necessarily match any landscape feature (Fig. 8; Kölzsch *et al.* 2015). Fig. 8 also illustrates the fact that one could observe multi-scale movement independently of the resource distribution (e.g., multi-scale interpatch motion) and without specifically following landscape cues or memory. In this regard, the question of how exploratory movement behaviour may help organisms to gather key information about the environment and change prior expectations requires further research.
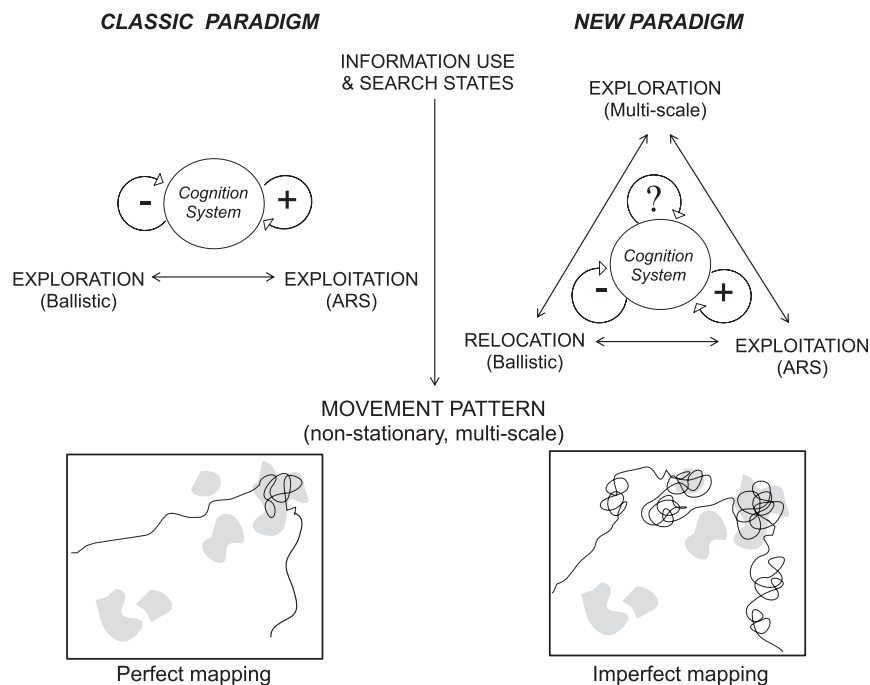
Figure 8 Depiction of the classic and the new foraging paradigms discussed, with two or three elementary motivational states (leading to three different movement modes), respectively. A general cognitive system establishes information fluxes and feedback with the external environment. The system measures information through its sensors, stores, processes, and interprets the information (with some internal modulation) to generate a positive, negative, or relatively more 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. Note: ARS = Area Restricted Search.

Future perspectives

The wide range of theoretical generative mechanisms of search (Reynolds 2015) makes discovering the true underlying biological mechanisms difficult (Bartumeus 2015). Moreover, the exact biological mechanisms may differ among organism according to their evolutionary history. In our view, the solution to better linking process to pattern in the study of foraging movement, and in particular, understanding how foraging organisms decide whether to capitalise on exploratory or exploitative movement strategies (Vergassola *et al.* 2007; Hein & McKinley 2012) is twofold. From an empirical perspective, the field needs to move from trajectory data collection to hypothesis-driven experiments and comparative analysis to evaluate search tradeoffs and important variations of scale across ecological contexts and species. From a modelling perspective, the field needs to move from statistical curve fitting and model selection (Colding *et al.* 2008; Smouse *et al.* 2010; Jansen *et al.* 2012; Reynolds 2012, 2014) to exploring the underlying universality among apparently different models (Frank 2014). Neither movement modelling discussions (Benhamou 2007, 2014; Humphries & Sims 2014) nor high-throughput movement data (Humphries *et al.* 2012; Raichlen *et al.* 2014) will be enough to disentangle pattern from process in animal foraging. Hypothesis-driven and large-scale manipulative experiments are required (Bartumeus 2015).

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

two other anonymous referees that thoroughly and critically reviewed previous versions of this manuscript.

AUTHORSHIP

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